TERRESTRIAL TETRAPOD COMMUNITIES OF THE LATE PALAEOZOIC: AN ICHNOLOGICAL PERSPECTIVE

by

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ABSTRACT

The Late Palaeozoic was an important period in the evolutionary development of terrestrial tetrapod communities. Carboniferous assemblages that comprised predominantly 'temnospondyl' stem-lissamphibians declined as the amniotes rose to dominance during the Permian. This transition is here charted from an ichnological perspective, using vertebrate trace fossil evidence from present day Europe and North America. The only comprehensive Late Carboniferous vertebrate trackway assemblage known from Europe, from Alveley, southern Shropshire (UK) represents the principal dataset for this study. The introduction of a new method for stabilising ichnotaxonomy through the use of phenetic, numerical methods facilitates the integration of European and North American ichnological classifications, and the material from Alveley extends the stratigraphical ranges of a number of ichnotaxa back from the Early Permian. Trackway data are correlated with body fossil data through the development of a protocol that uses a combination of phenetic and phylogenetic, or character-based, methods. This synthesis of evidence from skeletal material and trackway data enables the evolutionary development of early terrestrial tetrapod communities to be charted. On the basis of this new perspective, models proposed for the observed Late Palaeozoic vertebrate faunal turnover are reviewed, and a new model is formulated, bearing in mind that patterns of Late Palaeozoic lissamphibian and amniote diversity and abundance resulted from the interaction of intrinsic, biological processes with dynamic, extrinsic systems.

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INTRODUCTION

The Late Carboniferous to Early Permian represents a key stage in the evolution of tetrapod faunas. The amphibious assemblages of the Carboniferous declined with the appearance of the amniotes during the later stages of that period, producing a transition to predominantly terrestrial communities that continued into the Early Permian. Although the first land vertebrates only appeared during the Late Devonian (Clack 1997, 2002*a*; Coates 1996), by the Early Permian amniotes had become the dominant terrestrial forms, having diverged to form three major lineages: the Synapsida (stem-mammals); Diapsida (reptiles); and stem-Testudines, or turtles (Laurin and Reisz 1995).

The aim of this study is to chart the development of terrestrial tetrapod communities across this Late Palaeozoic faunal transition with the use of trace fossil evidence from present day Europe and North America. A number of objectives are undertaken to fulfill this aim:

- the palaeoenvironmental, palaeoecological, and systematic interpretation of the only comprehensive Late Carboniferous ichnological assemblage from Europe, which extends knowledge back from the Early Permian
- the introduction of a new technique for stabilising ichnotaxonomy through the use of phenetic, numerical methods
- the integration of European and North American ichnotaxonomy following a study of holotype material
- the development of a new protocol for correlating trackways with potential trackmakers, using a combination of phenetic and phylogenetic techniques
- Finally, the synthesis of these data to achieve the aim of examining the development of terrestrial tetrapod communities from a novel perspective.

Vertebrate trackways provide a considerable amount of data that is not supplied by skeletal material, and therefore enable a different approach to the study of community development. Faunal turnover has traditionally been examined through the use of estimates of taxonomic richness, and while these provide an indication of familial diversity through the fossil record, they do not provide a measure of absolute numbers of individuals. Trackway assemblages, representing a direct, *in situ* impression of taxa present, act as a proxy for abundances of individuals, and these data may give considerably different assessments of populations. Consequently, a synthesis of Late Palaeozoic trackway data enables an examination of taxon abundances and relative proportions of taxa within terrestrial communities, from which the processes and patterns associated with adaptive radiation, taxon displacement and faunal turnover can be assessed. This novel use of trackway data in conjunction with body fossil data has the potential to greatly increase our understanding of terrestrial community

dynamics, as well as offering insight into periods of evolutionary transition from a completely new perspective.

A Late Carboniferous (Moscovian; Westphalian D) ichnological assemblage from the Salop Formation (former Keele Beds) of the Warwickshire Group, southern Shropshire, UK, forms the principal data set for the project. The tetrapod ichnofauna of Alveley, southern Shropshire, is the only vertebrate trackway assemblage of Late Carboniferous age in Europe. The material is representative of the Late Carboniferous to Early Permian transition within vertebrate communities, from the dominance of amphibians to that of amniotes, as it includes trackways made by a variety of primitive tetrapods of amphibian and reptilian grades. The numerous specimens of exceptionally well-preserved vertebrate trackways can be readily compared with Early Permian vertebrate ichno-assemblages from Germany, France and northern Italy. Preliminary studies of this ichnofauna were undertaken by Haubold and Sarjeant (1973, 1974), who recognised six ichnospecies within five ichnogenera (*Ichniotherium willsi*, *Dimetropus salopensis*, *Limnopus rawi*, *Batrachichnus alveleyensis*, *Anthichnium major* and *A. salamandroides*), based upon a selection of the better preserved material. However, due to advances in the understanding of vertebrate ichnology over the last thirty years, the ichnofauna is in need of revision. This study utilises all the available material, amounting to over 2400 individual footprints within 203 trackways, to build on Haubold and Sarjeant's initial work and provide the first comprehensive review of the ichno-assemblage.

Chapter 1 examines the Salop vertebrate ichno-assemblage in conjunction with other elements of the fauna, including plants, invertebrate traces and sedimentary structures, to facilitate a rigorous palaeoenvironmental and palaeoecological interpretation of a Late Carboniferous terrestrial habitat. Trackways are particularly useful in studies of this kind, as they enable fairly accurate estimates of, for example, community structure, in terms of taxa present, and the relative proportions of different groups within the community; abundance of individuals of a single taxon; the preferred habitats, or ecological niches, of certain taxa; the range of body sizes both within populations and single taxa; and possible taxon interactions, such as predation (e.g. Lockley and Madsen 1993: Kramer *et al.* 1995). Additionally, because trackways are formed within the habitat occupied by the trackmaker taxon, they can help to determine the role of environment, as well as stratigraphic age, in influencing the habitat choices of certain taxa, and furthermore, the distribution of these taxa within different sedimentary environments.

One of the greatest problems in utilising vertebrate trackway data stems from unsatisfactory ichnotaxonomy. Due to the range of preservational variants arising from differences, for example, in slope angle, method of preservation and trackmaker behaviour, traditional taxonomic methods have frequently produced unstable ichnotaxonomies, with a tendency towards oversplitting. An objective of

this study is therefore to provide a multivariate, statistical, non-biased approach to vertebrate ichnotaxon identification, which is repeatable and as stable and objective as possible (Chapter 2). With the use of this method, ichnotaxon diagnoses can be revised and tightened, and the placement of undescribed trackways into certain groups is controlled. This stabilization of vertebrate ichnotaxonomy, together with the resulting assessment of ichnotaxonomic diversity, enables a clearer palaeoecological interpretation of the Alveley fauna, and more accurate comparisons with other vertebrate ichnofaunas and known skeletal assemblages.

All terrestrial tetrapod body and trace assemblages of the Late Carboniferous and Early Permian are found within an area that stretches across central North America, through Britain, into southern France, Germany and the Czech Republic. This region closely mirrors the position of the Permian equator in relation to pre-drift Europe and North America (Ziegler 1990), indicating a palaeotropical distribution of terrestrial tetrapods along the southern margin of the single Euramerican continent, Laurasia, during this period. An absence of aquatic barriers enables the uniform distribution of these faunas across this region. Therefore, the North American and European faunas are comparable, with the European fauna representing a small section of the North American fauna. However, despite the similarity of these assemblages, separate ichnotaxonomic classifications have developed in Europe and North America, thereby impeding identification from the literature of North American ichnotaxa that are equivalent to those in Europe. Following the examination of many North American and European vertebrate ichno-assemblages, and in particular, holotype material, the systematic revision of Alveley ichnotaxa in Chapter 3 contributes to the integration of North American and European ichnotaxonomy.

Insight into palaeofaunas is greatly improved if trackway data can be integrated and compared with information from vertebrate body fossil assemblages. The preservation of biogenic sedimentary structures, such as footprints, and skeletal material is favoured by different conditions, and the two types of remains are infrequently found together. Trackways and body fossils thereby provide complementary information, which if combined, has the potential greatly to increase our understanding of terrestrial vertebrate communities. Chapter 4 outlines a method of associating trackways and trackmakers with the use of phylogenetic techniques, and examines the taxonomically hierarchical level to which the two types of preservation can be correlated.

Finally, all the data gleaned from this study, including revised trackway data from localities in central Europe and North America, are synthesised in Chapter 5 to chart the development of terrestrial tetrapod communities through the Late Palaeozoic. A number of hypotheses regarding the processes involved in the observed faunal turnover and taxon displacement throughout this period are considered, and an explanation offered for the patterns exhibited by trackway data.

CHAPTER 1

LATE CARBONIFEROUS TERRESTRIAL PALAEOENVIRONMENTS AND PALAEOECOLOGY: MOSCOVIAN ASSEMBLAGES FROM SOUTHERN SHROPSHIRE, UK

The extensive ichnofaunal and floral material of the Salop Formation (Moscovian; Westphalian D–Stephanian), southern Shropshire, UK is an important assemblage in terms of understanding Late Carboniferous terrestrial communities. Although key localities such as Joggins, Nova Scotia, Linton, Ohio, Mazon Creek, Illinois and Nýřany, Czech Republic have improved our knowledge of such associations (e.g. Carroll 1966, 1967; Nitecki 1979; Milner 1980, 1987; Baird *et al.* 1985; Hook and Ferm 1985), Late Carboniferous terrestrial assemblages remain rather poorly represented in the fossil record. However, this period is crucial to an understanding of terrestrial community development, as it incorporates a transition from typically wet, humid environments to the dry, semi-arid climates of the Permian (Witzke 1990; Ziegler 1990; Beauchamp 1994). This change greatly influenced community development within all sectors of Late Palaeozoic populations. For example, vertebrate communities changed from populations comprising predominantly amphibious forms (stem-lissamphibians, or 'temnospondyls') to those dominated by 'reptilian' total-group amniotes (Carroll 1988). A transition also occurred within lowland floral assemblages during the Late Carboniferous, from a domination of lycophytes to marattialean tree ferns (Phillips *et al.* 1985; DiMichele and Phillips 2002). Consequently, an understanding of terrestrial communities and relationships across this important transitional period is vital to an understanding of the evolution and development of early terrestrial ecosystems.

As the Salop assemblages include both vertebrate and invertebrate trackways, and floral remains, they enable a reconstruction of terrestrial community structure and biotic interactions within this important time period. In addition, the Salop ichnofauna constitutes the only comprehensive, well-preserved record of Late Carboniferous vertebrate trackways in Europe, and gives an important insight into the preferred ecological niches of represented vertebrate taxa. Together with sedimentary data, the large amount of fossil material enables a full interpretation of palaeoecology, palaeoenvironments, and depositional and preservational processes within a Late Carboniferous terrestrial ecosystem.

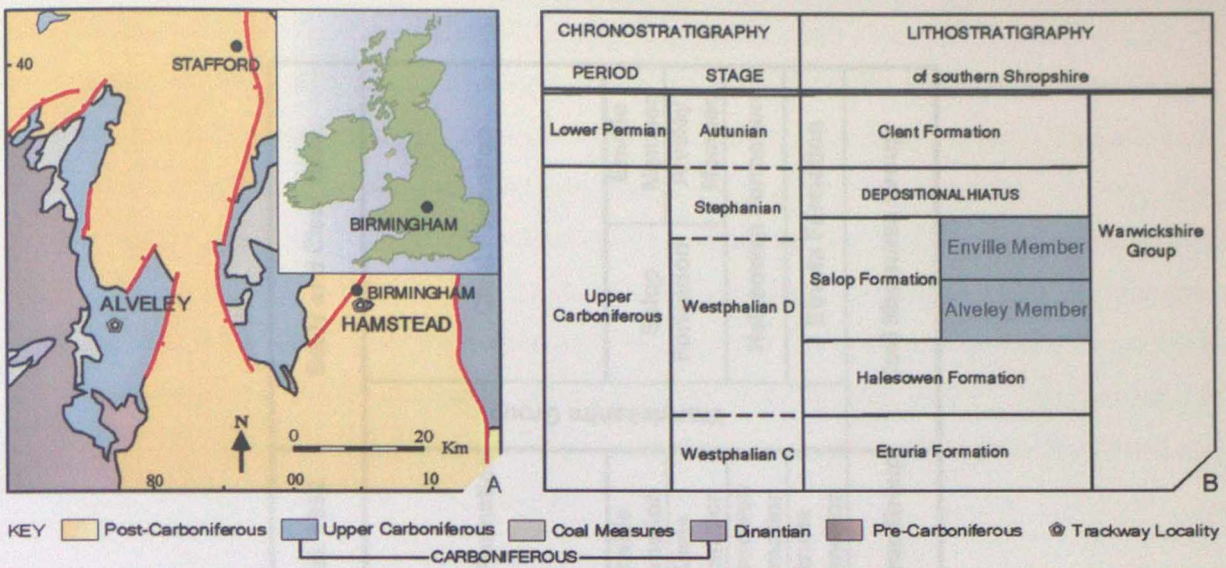
Location

The most extensive collections of vertebrate and invertebrate ichnofauna and flora were found within the Alveley Member of the Salop Formation (Warwickshire Group; Text-fig. 1.1B), at the Butts and Hall Close quarries, Alveley, southern Shropshire (SO 7556 8298 and SO 7605 8375 respectively; Text-fig. 1.1A). The first finds were made by Dr F. Raw in 1914, and a preliminary collection was made upon their discovery, although most of the material was collected in the spring and autumn of

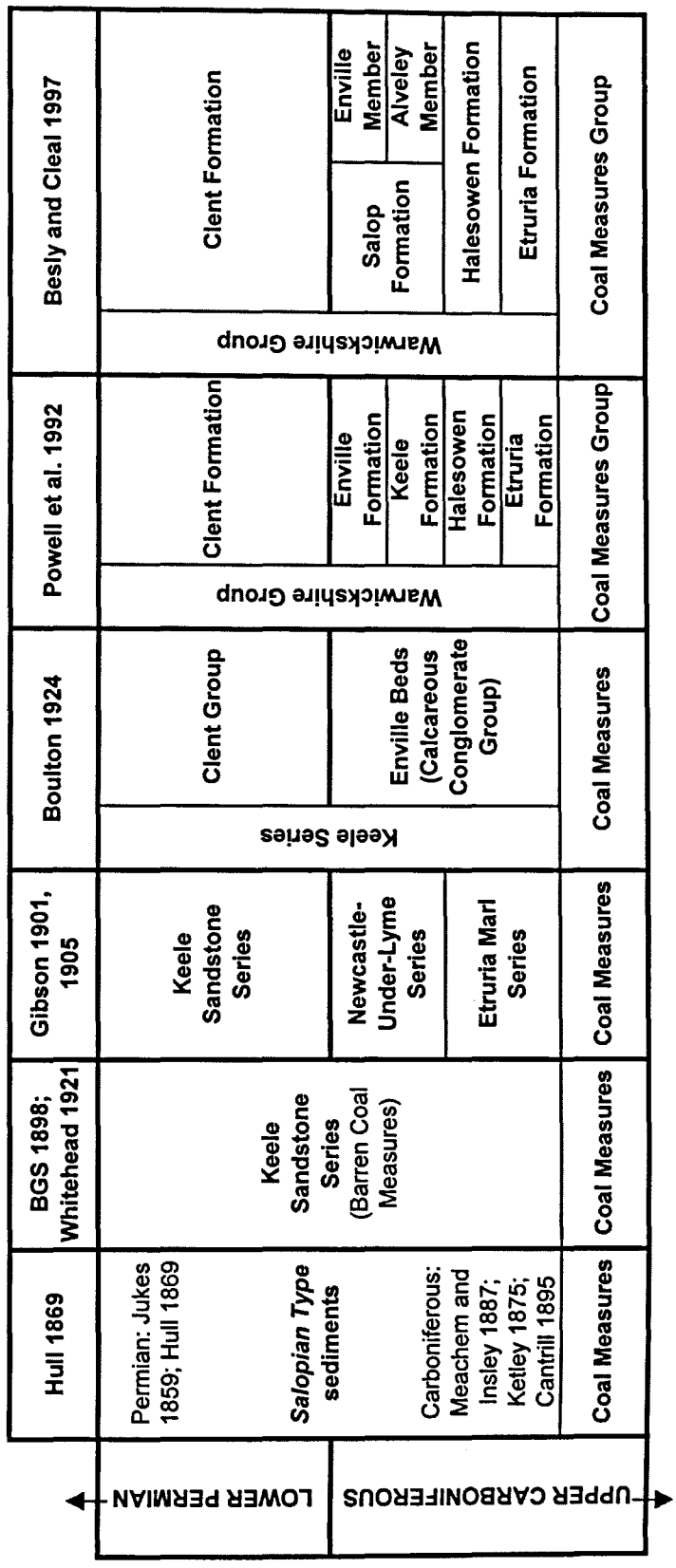
1919 (Lapworth Museum Archive, Miscellaneous Collection 60). Other, less extensive material was concurrently found in the Enville Member of the Salop Formation (Text-fig. 1.1B), at the now reclaimed New Quarry, Hamstead, south Birmingham (SP 0492 9265; Text-fig. 1.1A), and within the Slade Heath and Windsor Street No. 2 boreholes (SJ 9190 0710 and SP 0894 8931 respectively; Text-fig. 1.1A). All material has since been housed in the Lapworth Museum at the University of Birmingham, UK, and at the British Geological Survey, Keyworth, Nottingham, UK.

Stratigraphy

The red-bed sequence overlying the Carboniferous Coal Measures in Staffordshire and Shropshire was first defined by Jukes (1859) as being of entirely Permian age, and was described by Hull (1869) as comprising 'Lower Permian Salopian Type' sediments (Text-fig. 1.2). Meachem and Insley (1887), Ketley (1875), and Cantrill (1895) challenged this view, suggesting that the sequence was in fact of Carboniferous age, as indicated by the presence of thin coals and *Spirorbis* limestone horizons; this proposal was supported by the palaeobotanical studies of Kidston (1888), and later by those of Gibson (1901, 1905). Following remapping of the North Staffordshire coalfield by the British Geological Survey in 1898, the basal part of the 'Lower Permian Salopian Type' succession was identified as lying conformably upon the underlying Upper Coal Measures sequence. The lower part of the succession was consequently included within the latter stratigraphical unit, and renamed the 'Keele Sandstone Series' (Whitehead 1921), also known as the 'Barren Coal Measures' (Powell *et al.* 2000). The Keele Sandstone Series was later redefined to include only the youngest sediments of the red-bed succession, overlying the older Newcastle-Under-Lyme and Etruria Marl Series, and was regarded as the lowest unit of the Permian (Gibson 1901, 1905). This stratigraphy was based upon the sediments of the North Staffordshire Coalfield, but was applied to the entire West Midlands. However, the recognition of an unconformable boundary within the Keele Series by Boulton (1924) led to its division into two thinner sequences, the Enville Beds, or Calcareous Conglomerate Group, considered to be the uppermost unit of the Carboniferous, and the overlying Clent Group, regarded as Permian in age. More recent mapping of southern Staffordshire (Powell *et al.* 1992) led to the further division of the Keele Series into five distinct units, named the Etruria (50–300 m in thickness), Halesowen (70–350 m), Keele (50–247 m), Enville (100–247 m), and Clent (138–240 m) formations (from oldest to youngest), together constituting the Warwickshire Group. The British Geological Survey rock lexicon (www.bgs.ac.uk/scripts/lexicon) suggests that the upper part of the Salop Formation is Lower Permian in age, however, all published material to date indicates that the Clent Formation remains the lowest unit of the Permian in the West Midlands (e.g. Glover and Powell 1996; Besly and Cleal 1997; Powell *et al.* 2000; Text-fig. 1.2).



TEXT-FIG. 1.1. A, Geological map of the South Staffordshire Coalfield, UK (after Glover and Powell 1996), showing the geographical position of the Alveley and Enville (Hamstead) trackway localities. B, stratigraphical classification of the Warwickshire Group in southern Shropshire (after Powell *et al.* 2000).



TEXT-FIG. 1.2. Stratigraphical history of the Warwickshire Group in southern Shropshire.

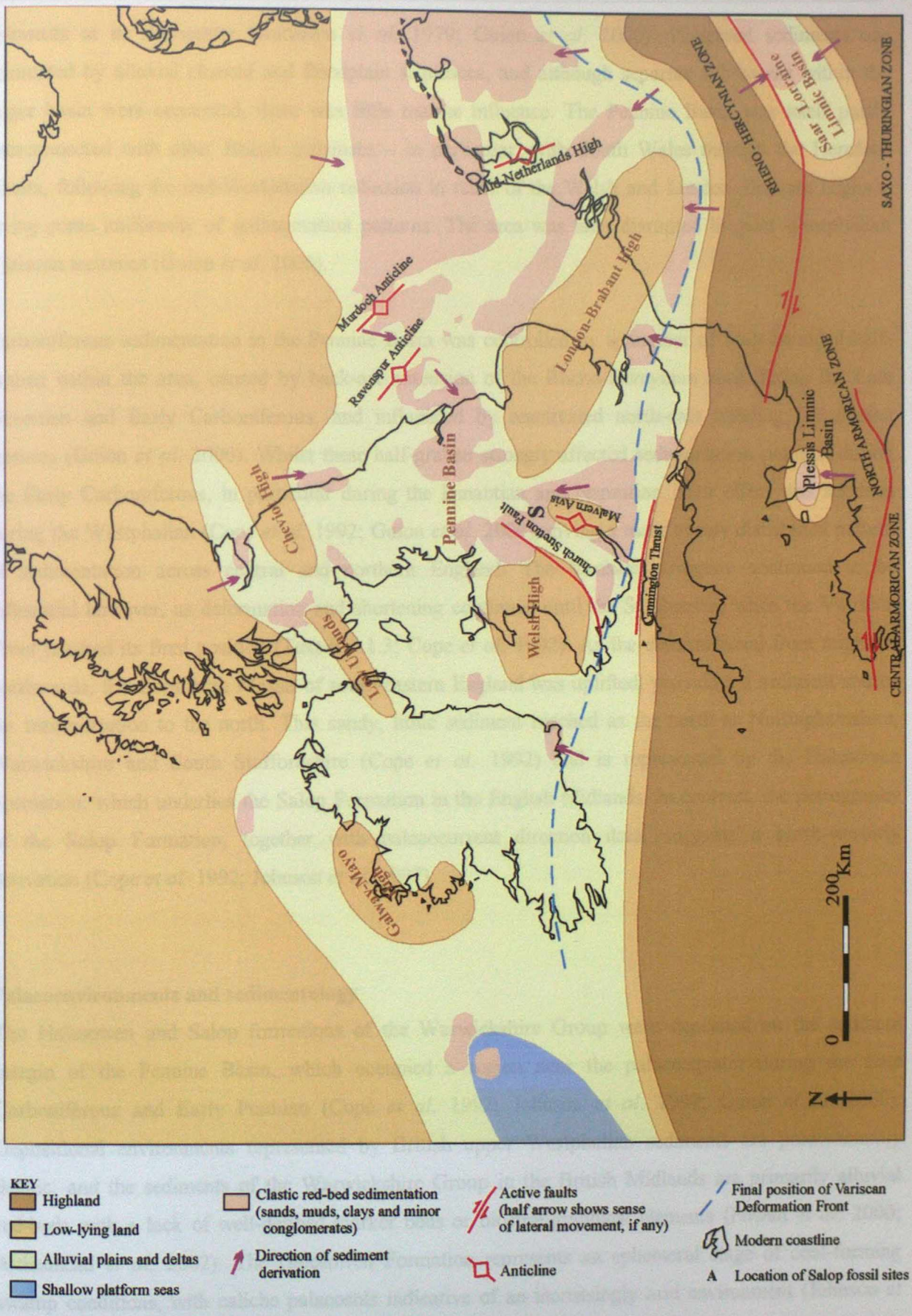
The Salop Formation and its two members (the lower Alveley Member and upper Enville Member) were introduced by Besly and Cleal (1997) following an amendment to the lithostratigraphy of Staffordshire and Shropshire based upon sandstone compositions, detrital clay mineral assemblages, and geophysical log responses. This new formation replaced the Keele and Enville formations of Powell *et al.* (1992), and more closely reflects changes in provenance and palaeogeography. The Alveley Member has a relatively low sandstone content, whilst the Enville Member is sandstone-rich (Besly and Cleal 1997; Johnson *et al.* 1997) and includes Carboniferous limestone clasts and lenticular conglomerates (those which gave the Calcareous Conglomerate Group its now obsolete name; Wills 1948; Besly and Cleal 1997). The entire Salop Formation up to the base of the Clent Formation is regarded as Moscovian (Westphalian D); this is supported by evidence from palaeobotanical and palynological studies (McNestry 1994; Besly and Cleal 1997).

Palaeogeographical and depositional setting

Tectonic activity associated with the Variscan Orogeny was the principal control upon Late Carboniferous tectonics and sedimentation in Britain. A large mountain belt running from Russia, across Western Europe and into North America was created as the African section of Gondwana collided with European Laurasia during the Early Carboniferous (Guion *et al.* 2000). An associated northward-dipping subduction zone, running through central France and northern Germany, was bounded to the present north by the Rheno-Hercynian zone. This consisted of a back-arc seaway floored by oceanic crust, which stretched across southwest England into northern France and Germany (Guion *et al.* 2000). Although Britain lay to the north of the collisional zone, on a foreland dominated by sedimentary basins, the Variscan Orogen controlled its geological evolution, especially during the Carboniferous.

During the Late Carboniferous, Britain was divided into three areas of deposition upon the Rheno-Hercynian foreland, separated by the Welsh–London–Brabant High and the Southern Uplands High. These long standing palaeogeographical barriers split Britain into five separate provinces, each with a distinctive tectonic and sedimentary history (Guion *et al.* 2000). Southern Shropshire, the area of present study, formed part of the largest and best-documented sedimentary region, the Pennine Basin, which lies north of the Welsh–London–Brabant High, and stretches from southeast Ireland, across central England into Belgium (Text-fig. 1.3; Cope *et al.* 1992).

To the north of the Pennine Basin lay the Southern Uplands High, which stretched across northern Britain into the North Sea as the Cheviot, or Mid-North Sea High and into Ireland as the Low Uplands, or Longford-Down Massif (Cope *et al.* 1992; Guion *et al.* 2000). The Pennine Basin encompasses central and northern England, continuing laterally into the North Sea, and preserves over 2800 m of



KEY

- Highland
- Low-lying land
- Alluvial plains and deltas
- Shallow platform seas
- Clastic red-bed sedimentation (sands, muds, clays and minor conglomerates)
- Direction of sediment derivation
- Active faults (half arrow shows sense of lateral movement, if any)
- Anticline
- Final position of Variscan Deformation Front
- Modern coastline
- A Location of Salop fossil sites

TEXT-FIG. 1.3. Palaeogeographical map of Britain during the Moscovian (Westphalian D; c. 302 Ma). After Cope *et al.* (1992).

sediments at its depocentre (Anderton *et al.* 1979; Guion *et al.* 2000). Preserved sediments are dominated by alluvial channel and floodplain sequences, and although separate sub-basins within the larger basin were connected, there was little marine influence. The Pennine Basin was itself partly interconnected with other British provinces – in particular, with South Wales through the Hereford Straits, following the mid-Westphalian reduction in relief of the Welsh and London–Brabant Highs – giving some uniformity of sedimentation patterns. The area was later disrupted by post-Westphalian Variscan tectonics (Guion *et al.* 2000).

Carboniferous sedimentation in the Pennine Basin was controlled by a number of fault-bounded half-graben within the area, caused by back-arc extension of the Rheno-Hercynian zone during the Late Devonian and Early Carboniferous, and influenced by reactivated north-east trending Caledonian features (Guion *et al.* 2000). Whilst these half-graben strongly affected sedimentation patterns during the Early Carboniferous, in particular during the Dinantian and Namurian, their effect was subdued during the Westphalian (Cope *et al.* 1992; Guion *et al.* 2000), giving a more evenly distributed pattern of sedimentation across central and northern England. The Variscan Orogeny continued to be influential however, as deformation and shortening continued until the Stephanian, when the Variscan Front reached its final position (Text-fig. 1.3; Cope *et al.* 1992). As the deformational front migrated northwards, the Cornubian Massif of south-eastern England was uplifted, providing a sediment source for transportation to the north. This sandy, lithic sediment reached as far north as Nottinghamshire, Warwickshire and South Staffordshire (Cope *et al.* 1992) and is represented by the Halesowen Formation, which underlies the Salop Formation in the English Midlands. In contrast, the petrography of the Salop Formation, together with palaeocurrent direction data, suggests a north-westerly derivation (Cope *et al.* 1992; Johnson *et al.* 1997).

Palaeoenvironments and sedimentology

The Halesowen and Salop formations of the Warwickshire Group were deposited on the southern margin of the Pennine Basin, which occupied a region near the palaeoequator during the Late Carboniferous and Early Permian (Cope *et al.* 1992; Johnson *et al.* 1997; Guion *et al.* 2000). Depositional environments represented by British upper Westphalian sediments are predominantly deltaic, and the sediments of the Warwickshire Group in the British Midlands are primarily alluvial red-beds with a lack of well-defined marker beds or biostratigraphical elements (Powell *et al.* 2000; Aitkenhead *et al.* 2002). The Halesowen Formation represents an ephemeral stage of coal-forming swamp conditions, with caliche palaeosols indicative of an increasingly arid environment (Johnson *et al.* 1997). Mudstones and siltstones dominate, with minor sandstones, *Spirorbis* limestones, and dark grey shales that bear bivalves, ostracods and fish faunas (Aitkenhead *et al.* 2002). This formation

conformably underlies the Salop Formation, which comprises the Alveley and Enville members, discussed below.

Stratigraphy and sedimentology of the Alveley Member (Moscovian; Westphalian D)

The unit is the lowest stratigraphical division of the Salop Formation (Warwickshire Group; formerly the 'Barren Coal Measures') in the Staffordshire and Shropshire area (Text-fig. 1.1B; Besly and Cleal 1997; Powell *et al.* 2000). The type area includes quarries and stream sections near Alveley, Shropshire, along the River Severn to the Bobbington region (SO 7583 to SO 7784), and contains 152–247 m of Moscovian (Westphalian D) sediments (Besly and Cleal 1997; Johnson *et al.* 1997; Powell *et al.* 2000). Reference sections listed by Powell *et al.* (2000) are the Daleswood Farm Borehole (SO 9511 7913, from 147.4 to 97.7 m depth; complete, continuous borehole core; Text-fig 1.4) and the Alveley No. 1 Borehole (SO 7818 8608, from surface to 76.8m depth; retained as selected hand specimens).

The full thickness of the Alveley Member is known only from the Daleswood Farm Borehole core, where it is 49.7 metres thick (SO 9511 7913, from 147.4 to 97.7 m depth; Powell *et al.* 2000). The relevant sections have been re-logged at centimetre-scale (Text-fig. 1.4). At outcrop, only the sandstone-rich parts of the sequence are exposed, and are up to nine metres thick. This is presumed to be the base of the Alveley Member, since in the Daleswood Farm Borehole only the basal section preserves equally thick sandstone sequences. This correlation is a reasonable assumption, as exposure demonstrates that these sandstone beds are laterally persistent over large, kilometre-scale areas, and change little in thickness. Two facies associations are recognised; these are described below. A composite log from the type area (Alveley Quarry, SO 7582 8482, and Hextons Quarry, SO 7586 8184; Text-fig. 1.5) illustrates a further two lithofacies within Facies Association AA.

Facies Association AA: observations

The basal and upper middle parts of the Alveley Member are composed of a coarse to medium-grained, red and purple lithic arenite, with thin intercalating mudstone horizons that contain weakly developed, caliche palaeosols. Low angulation cross-strata and erosional bed bases are typical of this facies association, and both individual sandstone and mudstone horizons are sheet-like, being laterally traceable over several kilometres. The arenites are interspersed with thin, white and black *Spirorbis* limestone horizons, in association with clay bands comprising illite and kaolinite (Besly and Cleal 1997). The association comprises two distinct but related lithofacies. The first, Lithofacies AA1, is dominated by lenticular, concave-up bar forms, composed of consistently medium-grained lithic arenite (Text-fig. 1.6). These comprise low and increasing angulation bedload sheets, with clear bar reactivation surfaces. This section is topped with a distinct marker-bed, a laterally persistent mudstone horizon within which desiccation cracks, and possibly also vertebrate trackways, are preserved. These

appear as casts upon the base of the overlying sandstone bed. The second lithofacies, AA2 (Text-fig. 1.7) comprises highly channelised, fining upwards coarse and medium-grained lithic arenite beds, exhibiting low angulation cross-strata. Erosional, channelised bed bases cut through the underlying sediments with a palaeotopography of up to two metres. The sequence fines upward throughout, and intercalated mudstone horizons become increasingly frequent up-section.

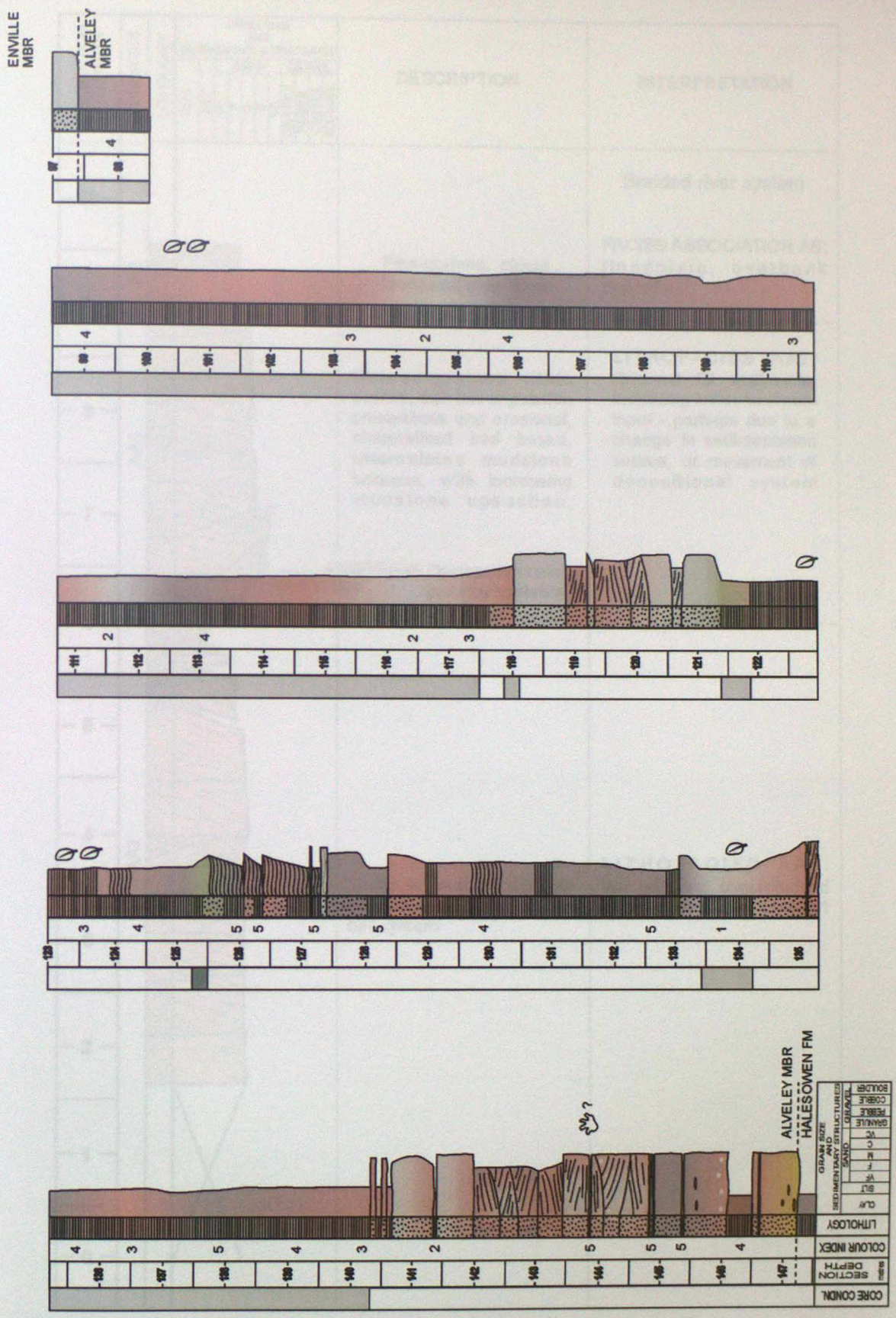
Facies Association AB: observations

Facies Association AB dominates the Alveley Member. The description and interpretation of this association is based upon the Daleswood Farm Borehole core, since it is not present at outcrop. Due to the nature of the sediment, it is in poor condition, even in the core, through a large part of the finer-grained material. Nevertheless, it can be seen that this facies association comprises red and purple massive, planar-laminated, and ripple-laminated mudstones, with occasional coarsening-upwards sequences to very fine-grained, ripple and planar-laminated lithic arenites. Some cyclicity of deposition is evident from the colouration of the mudstone horizons; this can be used as a proxy for the level of sub-aerial exposure and consequently also palaeosol maturity. Cycles consist of sequences of increasing exposure and palaeosol development over a scale of four to seven metres.

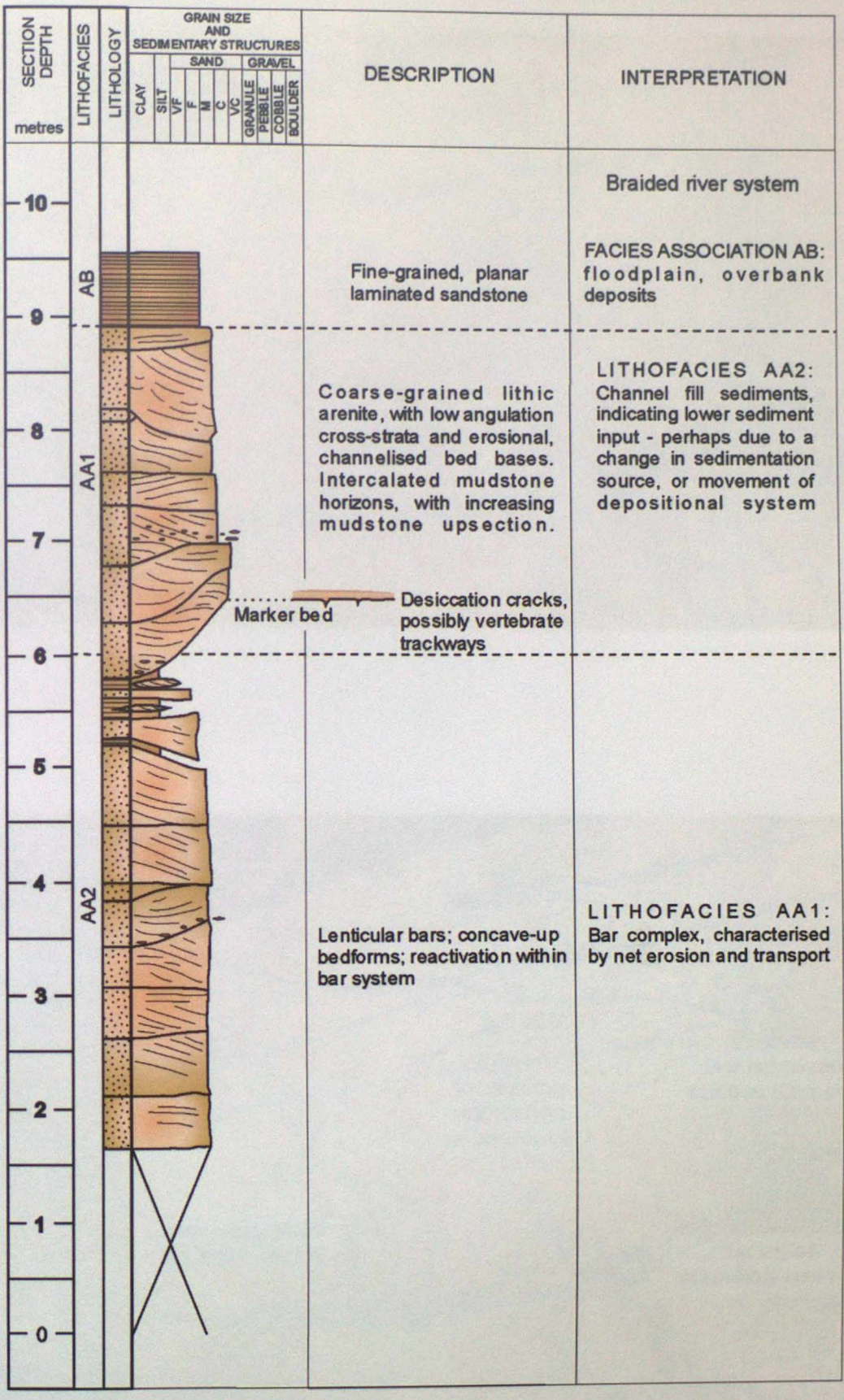
Alveley Member: facies interpretation

Sediments of the Alveley Member are those of an alluvial floodplain dominated by a fairly mobile, braided river system. The two main facies associations comprise channel belt, and overbank, floodbasin deposits. The channel belt sequence (Facies Association AA), characterised by low angulation cross-strata and erosional bed bases, comprises two lithofacies, representing distinct but interrelated depositional environments. The first, Lithofacies AA1, represents deposition within an extensive bar complex, characterised by net erosion and transport. Glover and Powell (1996) suggested the presence of a persistently high water table during the deposition of this succession. The second lithofacies, AA2, represents channel fill sedimentation within the channel belt system, indicative of decreased sediment input, perhaps due to a change in sediment source, or movement of the depositional system. Facies Association AB is interpreted as representing overbank, or flood basin sedimentation, with sandstone horizons possibly representative of crevasse splay deposits. A rigorous interpretation of Facies Association AB cannot be made with any certainty due to the poor condition of the core material and the lack of current exposure in the field.

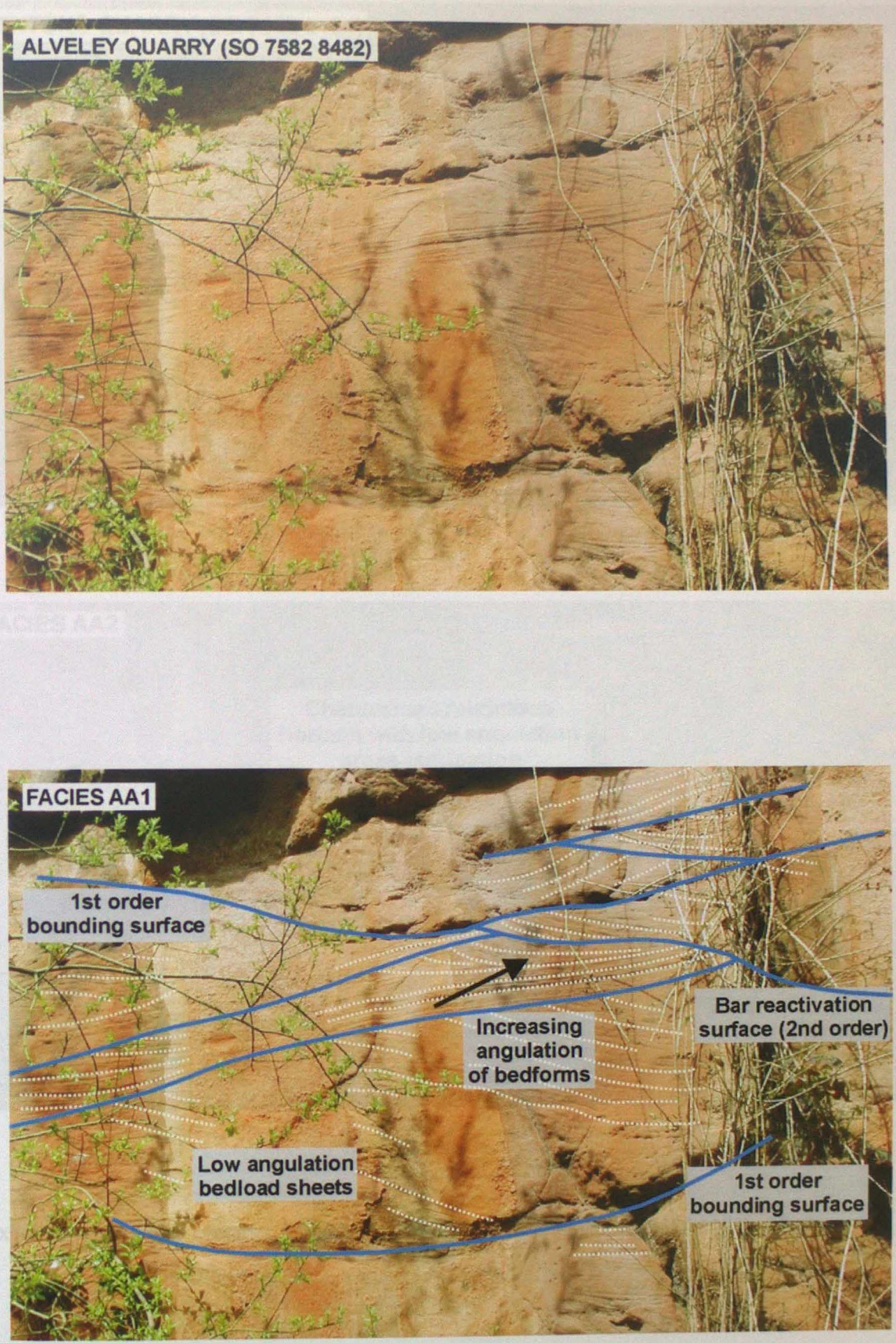
Throughout the Alveley Member, a change in depositional rates is evident, from rapid, high-energy deposition within the basal part to slow, low-energy deposition throughout most of the remainder of the sequence, perhaps as the river system moved over time. Periodic decreases in sediment input level are also observed within the sandstone-rich, lower part of the member; these are postulated to be a result of either short-term movement of the river system, or a change in sediment source. Fluctuating



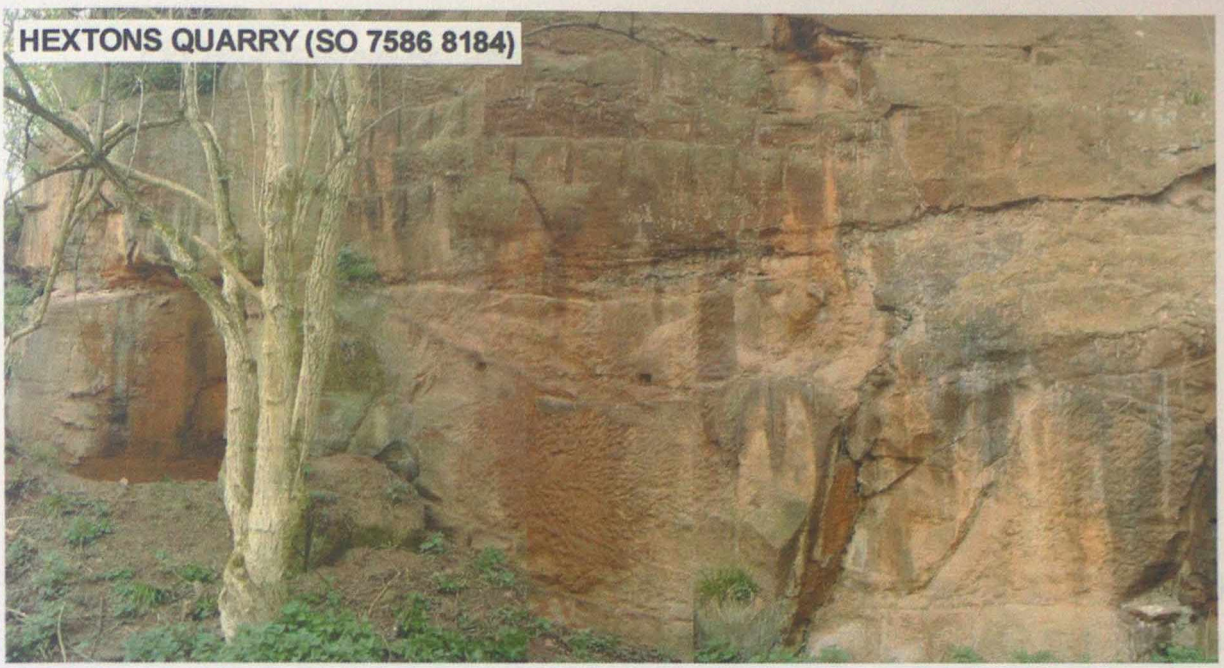
TEXT-FIG. 1.4. Sedimentary log of the Alveley Member, Salop Formation, Warwickshire Group. Daleswood Farm Borehole, from 147.4 to 97.7 m depth, SO 9511 7913. For full explanation see Text-fig. 1.10.

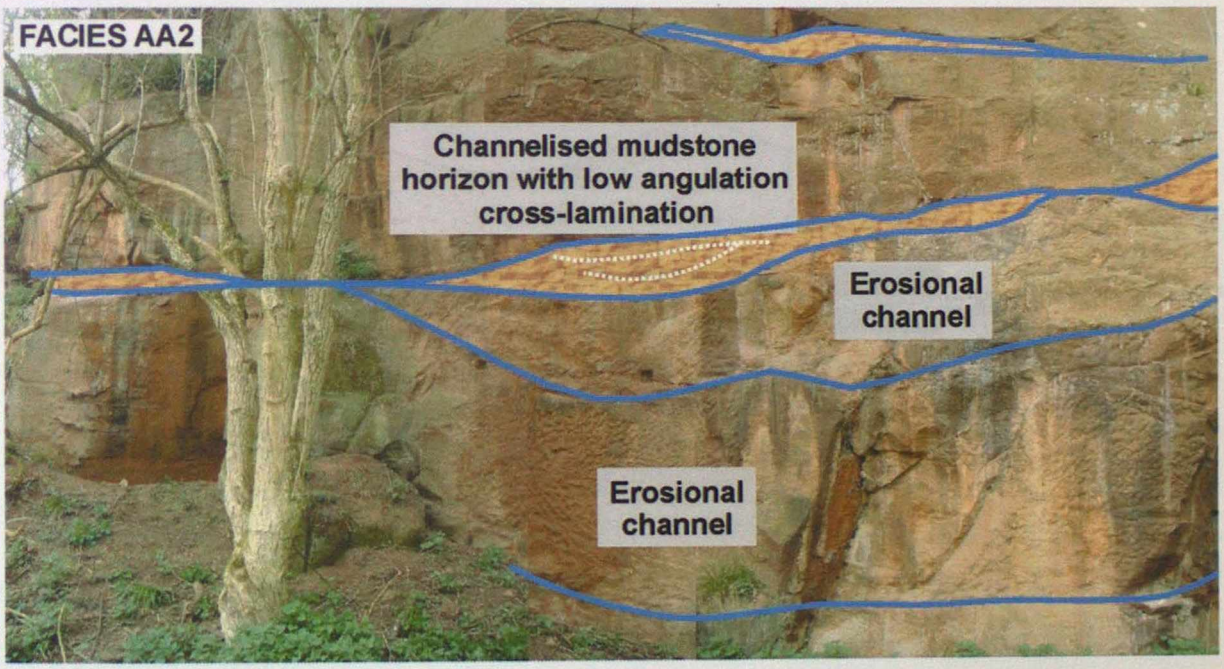


TEXT-FIG. 1.5. Sedimentary log of the lower part of the Alveley Member, Salop Formation, Warwickshire Group. Composite log from type area (Alveley Quarry, SO 7582 8482, and Hextons Quarry, SO 7586 8184).

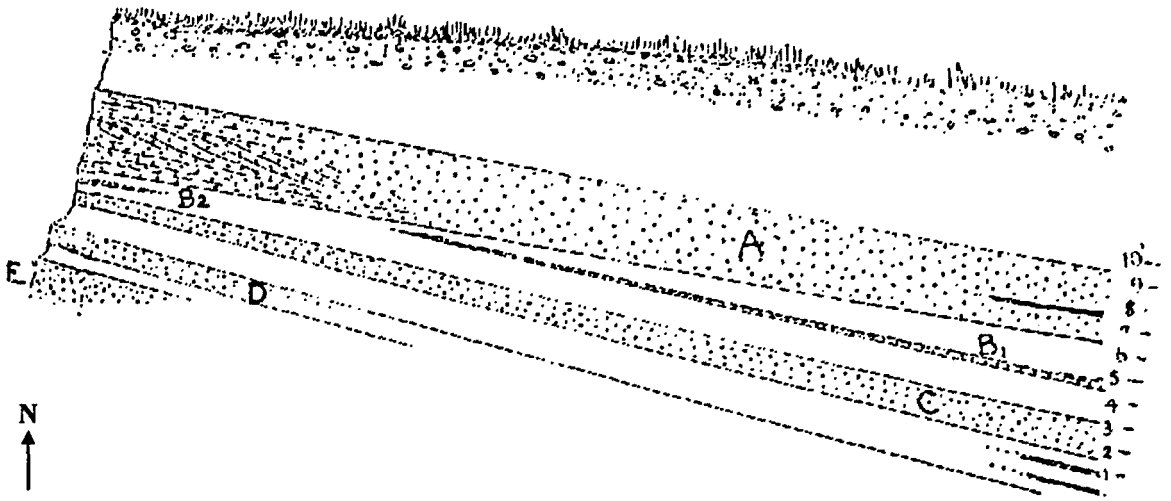


TEXT-FIG. 1.6. Alveley Member, Lithofacies AA1. Alveley Quarry (SO 7582 8482), Alveley.

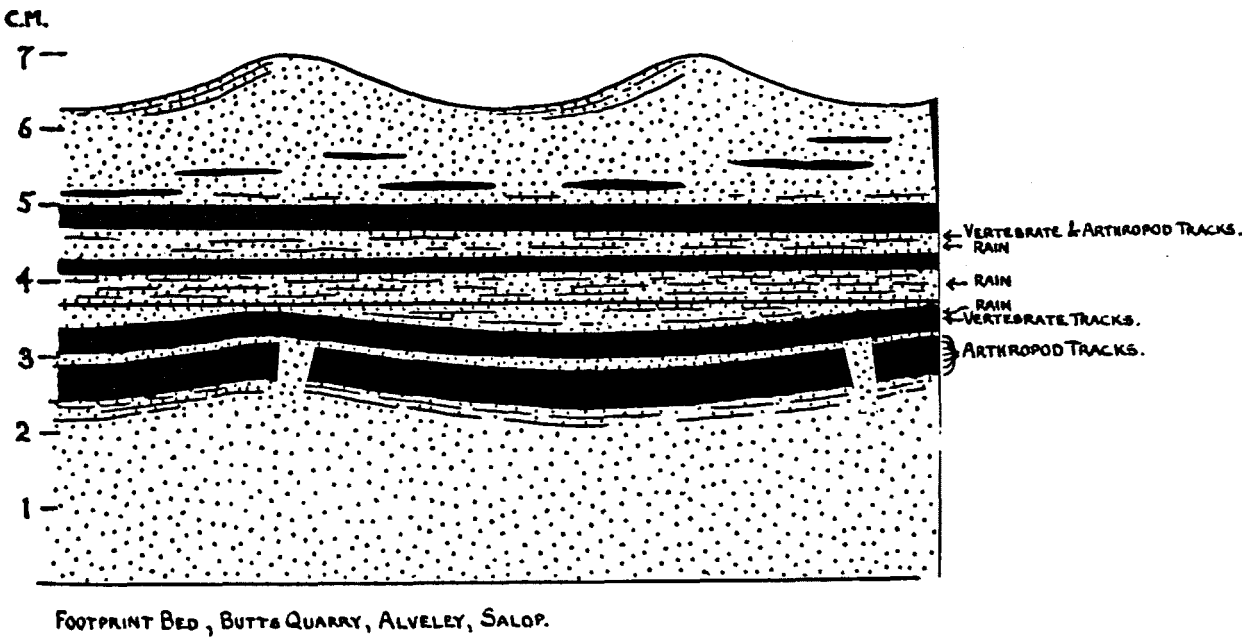




TEXT-FIG. 1.7. Alveley Member, Lithofacies AA2. Hextons Quarry (SO 7586 8184), Alveley.



TEXT-FIG. 1.8. Stratigraphical exposure of the Alveley Member at Butts Quarry (SO 7556 8298), as measured by Dr. F Raw (1919, Lapworth Museum Archive, Miscellaneous Collection 60). Raw's original sketch. Scale along eastern side of exposure, in feet. B_1 and B_2 denote the trackway horizon.



TEXT-FIG. 1.9. Structure of the trackway horizon within the Alveley Member at Butts Quarry (SO 7556 8298), as recorded by Dr. F Raw (1919, Lapworth Museum Archive, Miscellaneous Collection 60). Raw's original sketch. Scale along left hand side of sketch, in centimetres.

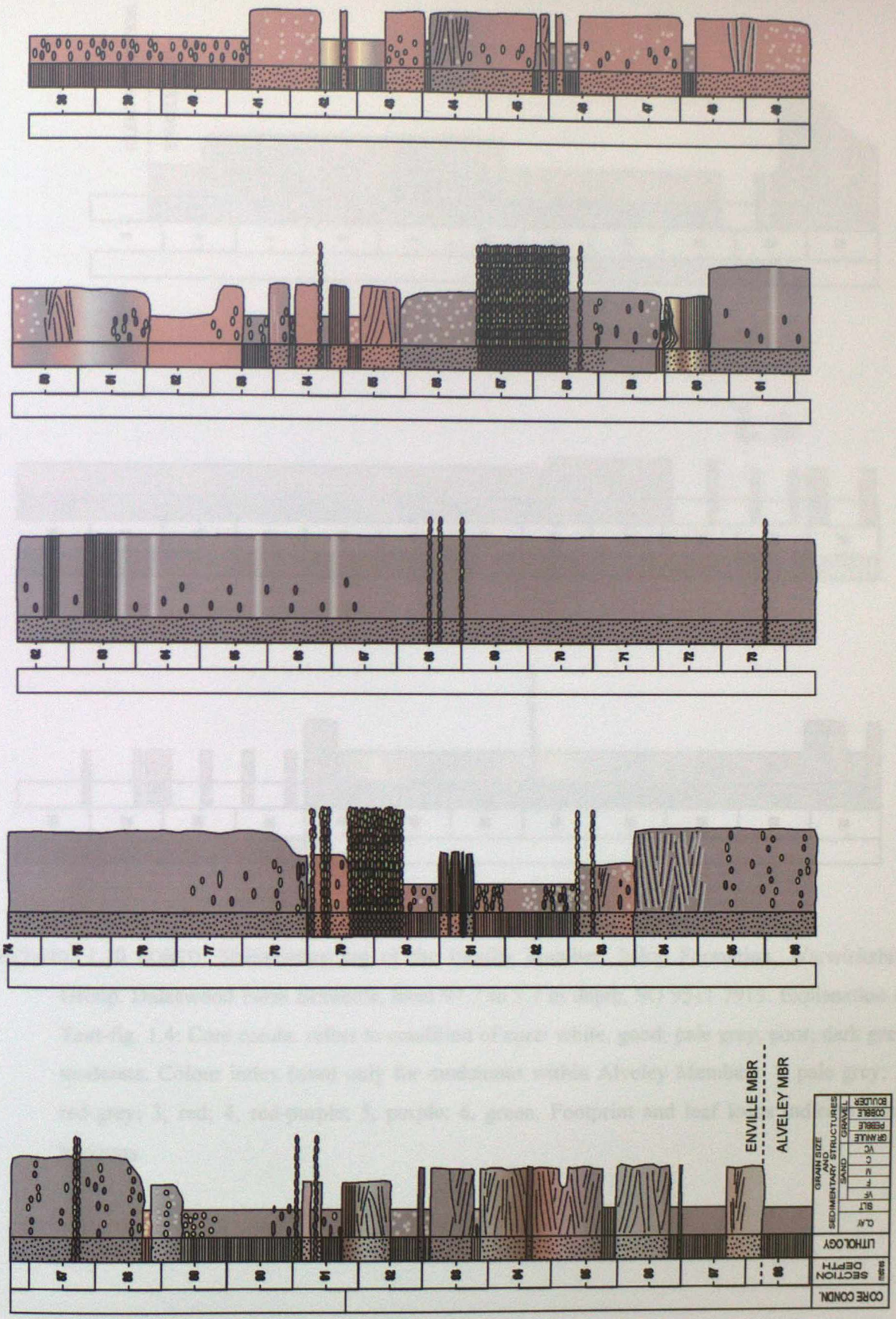
depositional rates within the channel belt are additionally apparent on a smaller time scale. The presence of vertebrate trackways suggests that in some cases these fluctuations occurred over very short periods of time such as days or weeks, producing flood overbank deposits and possibly crevasse splays. Furthermore, cycles of submergence and exposure upon the river levee and floodplain are suggested by the cyclicity of palaeosol maturity, as indicated by mudstone colouration, and the presence of terrestrial vertebrate and aquatic invertebrate trackways, raindrop imprints, and dessication cracks. *Spirorbis* limestones indicate deposition within shallow, ephemeral lakes within the floodplain region.

At Butts Quarry, where the Alveley vertebrate ichno-assemblage was collected, the succession at outcrop measures only 8 m and is at present poorly exposed, although Raw did log the fresh section in 1919 (Lapworth Museum Archive, Miscellaneous Collection 60; Text-fig. 1.8). Sediments here are of Lithofacies AA1. The ichnological material occurs as positive casts upon the bases of lithic arenite beds, although the 100 mm interval within which the material was found (Raw, unpublished manuscript, Lapworth Museum Archive, Miscellaneous Collection 60; Text-fig. 1.9) is no longer well exposed. Hall Close Quarry, which yielded plant material, has been completely reclaimed.

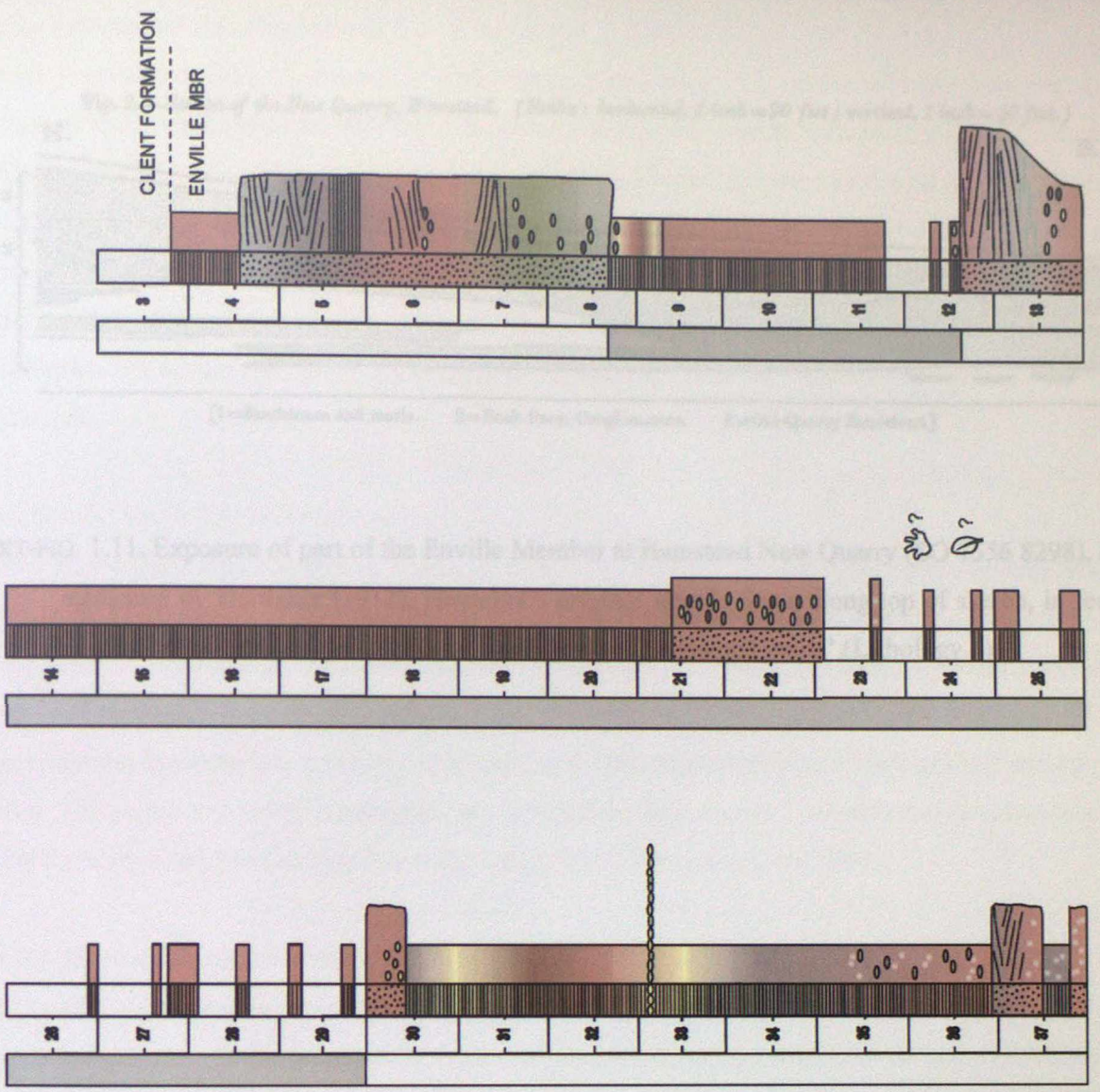
Stratigraphy and sedimentology of the Enville Member (Moscovian; Westphalian D–Stephanian)

This unit overlies the Alveley Member, forming the upper part of the Salop Formation (Text-fig. 1.1B; Besly and Cleal 1997; Powell *et al.* 2000). The type area lies between the villages of Enville (SO 78 87 to SO 80 88) and Alveley (SO 77 84 to SO 77 85; Powell et al. 2000). Two further reference sections are listed by Powell *et al.* (2000), namely the Daleswood Farm Borehole (SO 9511 7913, from 97.7 to 3.7 m depth; complete, continuous borehole core; Text-fig. 1.10) and the Romsley Borehole (SO 9501 7893, from 67.35 to 8.85 m depth; incomplete core sections, preserving upper part of member only).

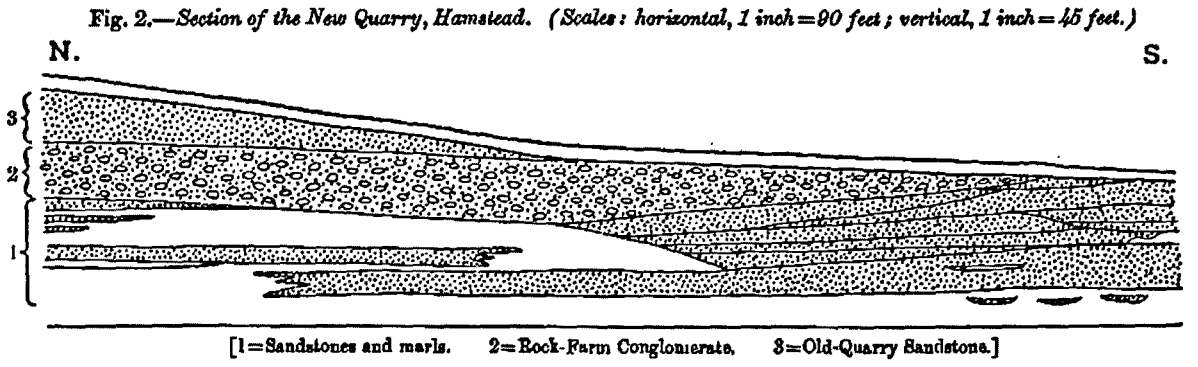
The Enville Member is represented most comprehensively by the Daleswood Farm Borehole core (SO 9511 7913, from 97.7 to 3.7 m depth; Powell *et al.* 2000), where it is 94 metres thick. Text-fig. 1.10 illustrates a log of this core at centimetre scale. Borehole records of the Slade Heath and Windsor Street No. 2 boreholes (BGS records SJ90 NW/5A, B and SP08 NE/852 respectively) make no mention of the horizons within which the palaeontological material was found. Hamstead New Quarry has now been fully reclaimed, but Hardaker (1912) described the sediments at this locality as dominantly purple marls with alternating, red and green sheet sandstones (Text-fig. 1.11). Vertebrate trackways and plant fossils appear mostly within thinly-bedded, lenticular sandstone beds of the upper Enville Member (New Quarry Marls) between approximately 22 m and 28 m depth within Daleswood Farm Borehole (Facies Association EB?; Text-fig. 1.10). Two facies associations are recognised within the Enville Member.



TEXT-FIG. 1.10. Sedimentary log of the Enville Member, Salop Formation, Warwickshire Group. Daleswood Farm Borehole, from 97.7 to 3.7 m depth, SO 9511 7913. For full explanation see below.



TEXT-FIG. 1.10 CONTD. Sedimentary log of the Enville Member, Salop Formation, Warwickshire Group. Daleswood Farm Borehole, from 97.7 to 3.7 m depth, SO 9511 7913. Explanation of Text-fig. 1.4: Core condn. refers to condition of core: white, good; pale grey, poor; dark grey, moderate. Colour index (used only for mudstones within Alveley Member): 1, pale grey; 2, red-grey; 3, red; 4, red-purple; 5, purple; 6, green. Footprint and leaf icons indicate fossil horizons.



TEXT-FIG. 1.11. Exposure of part of the Enville Member at Hamstead New Quarry (SO 7556 8298), as measured by Hardaker (1912). Hardaker's original sketch. Scale along top of sketch, in feet. The vertebrate trackways originated from the 'sandstones and marls' (Lithology 1).

Facies association EA: observations

Facies Association EA is comparable with Facies Association AA of the Alveley Member, and comprises red-brown, grey and red-purple, medium-grained lithic arenite with erosional bed bases and well-developed, small-scale trough cross-bedding. Minor, planar laminated mudstone horizons occur; these sometimes include small, dark purple mudstone clasts and pale grey, fine-grained calcretes and weakly developed palaeosols. These clasts also appear infrequently as bands within the arenite. Glover and Powell (1996) recognised thin, lenticular *Spirorbis* limestones, with brecciated textures. Facies Association EA occurs repeatedly throughout the Enville Member, but dominates the basal six metres of the unit.

Facies Association EB: observations

Facies Association EB, comprising coarser-grained, red, purple, grey and green-grey, homogeneous lithic arenite interspersed with thick, intraformational caliche conglomerates, dominates the remainder of the member. The arenite often contains imbricated mudflakes, or rip-up clasts, as well as rounded clasts of mudstone, very fine-grained arenitic material, and calcareous nodules (calcretes). The conglomeratic horizons are texturally immature, and clast-supported with a finer-grained red-purple matrix. Extraclasts are rarely imbricated, and predominantly comprise Carboniferous limestone, with minor Cambrian and Silurian quartz arenites (Wills 1948; Besly and Cleal 1997).

Enville Member: facies interpretation

The Enville succession is dominated by fluvial, channel belt deposits similar to those of the Alveley Member. Again, two facies associations represent deposition within distinct but related environments. Facies Association EA represents channel-fill sedimentation, whilst Facies Association EB is indicative of sheet-flood deposition. However, the higher sand content within the Enville Member is suggestive of either increased sediment input and/or less accommodation space in comparison with the Alveley Member, although a steady decrease in sediment grain size throughout the Enville Member indicates that this influence gradually diminished. This fining upwards trend, together with the smaller scale alternation of coarser and finer-grained sediment throughout the sandstone component of the member (Johnson *et al.* 1997), has been postulated to reflect a cycle of repeated tectonic uplift within the hinterland source region (Wills 1948; Johnson *et al.* 1997), which lay to the north (Cope *et al.* 1992; Johnson *et al.* 1997). Associated with the potentially reduced accommodation space and increased sediment input, the Enville Member exhibits a higher frequency of high energy flooding events, which are interspersed with long periods of floodplain exposure, as demonstrated by the dominance of facies association EB. This interpretation is supported by the presence of thick, homogeneous, coarse-grained lithic arenite beds with intraformational, caliche conglomerates that were probably derived from scouring of the muddy floodplain, and indicate extended periods of exposure to a semi-arid climate of the interfluves (Glover and Powell 1996; Johnson *et al.* 1997).

Sedimentary structures such as raindrop impressions and desiccation cracks were formed during these exposed periods. *Spirorbis* limestones suggest the presence of shallow, ephemeral lakes, formed as the channel belt region dried up after successive flooding events; the brecciated horizons within these limestones are indicative of fluctuating water levels (Glover and Powell 1996).

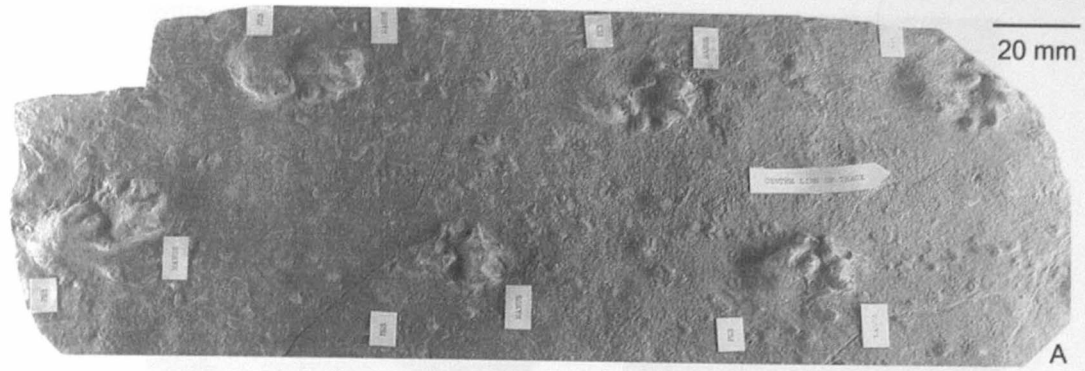
Fauna and flora of the Salop Formation

Palaeontological specimens were found within both the Alveley and Enville members, although the majority of material, consisting predominantly of tetrapod trackways and isolated footprints, was found within the Alveley Member at Butts Quarry (SO 7556 8298). Trackways of xiphosurans also occur on the bedding plane surfaces of some of these slabs, and sedimentary structures useful as environmental indicators (rippled beds, desiccation cracks and raindrop imprints) are present. Plant fossils are also found locally in the Alveley Member, for example, at Hall Close Quarry (SO 7605 8375), Alveley Quarry (SO 7582 8482) and within the Daleswood Farm (SO 9511 7913) and Alveley No. 1 (SO 7818 8608) Boreholes. A small number of vertebrate trackways and plant fossils were found within the Enville Member, at Hamstead, Birmingham (SP 0492 9265), and within the Slade Heath and Windsor Street No. 2 boreholes (SJ 9190 0710 and SP 0894 8931 respectively).

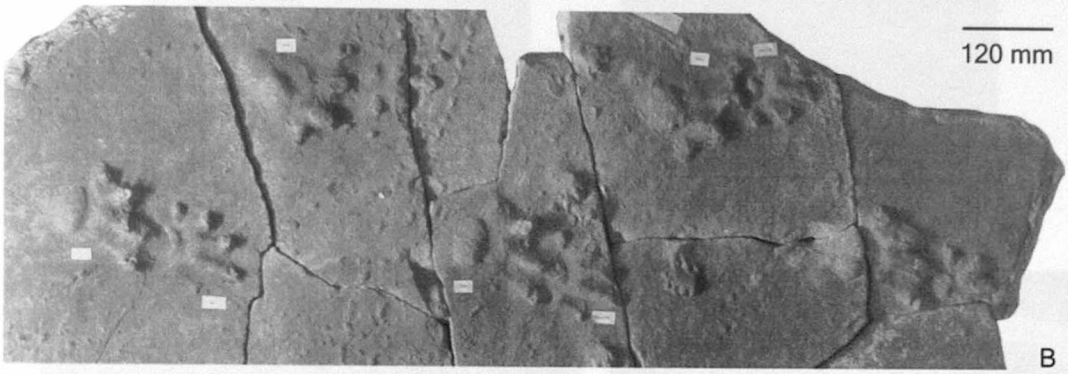
Vertebrates

The tetrapod ichnofauna of the Alveley Member is the only comprehensive vertebrate trackway assemblage of Late Carboniferous age in Europe. The material is representative of the Late Carboniferous to Early Permian transition within vertebrate communities, from the dominance of amphibians to that of amniotes, as it includes trackways made by a variety of primitive tetrapods of amphibian and reptilian grades. However, no skeletal material has as yet been discovered. In contrast, the Enville vertebrate trackway assemblage is small, and preserves only isolated footprints or single manus-pes sets. Nevertheless, the trace assemblages present are considerably different and offer an interesting comparison, providing evidence for palaeoenvironmental and palaeoecological variation between the Alveley and Enville members.

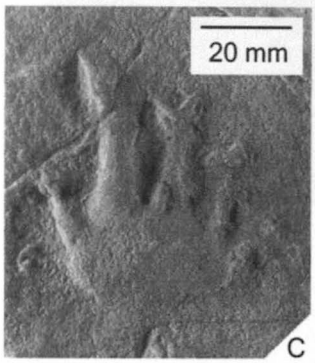
Preliminary studies of the Alveley ichnofauna were undertaken by Haubold and Sarjeant (1973, 1974), who recognised six ichnospecies within five ichnogenera (*Ichniotherium willsi*, *Dimetropus salopensis*, *Limnopus rawi*, *Batrachichnus alveleyensis*, *Anthichnium major* and *A. salamandroides*), based upon a selection of the better preserved material. However, due to advances in the understanding of vertebrate ichnology over the last thirty years, Tucker and Smith (in press; Chapters 2 and 3) have revised the ichnofauna with a study utilising all the available material, amounting to over 2400 individual footprints within 203 trackways. This builds on Haubold and Sarjeant's initial work and provides the first comprehensive review of the ichno-assemblage. The list of vertebrate ichnotaxa now comprises six ichnospecies within four ichnogenera (Text-fig. 1. 12). These have been identified



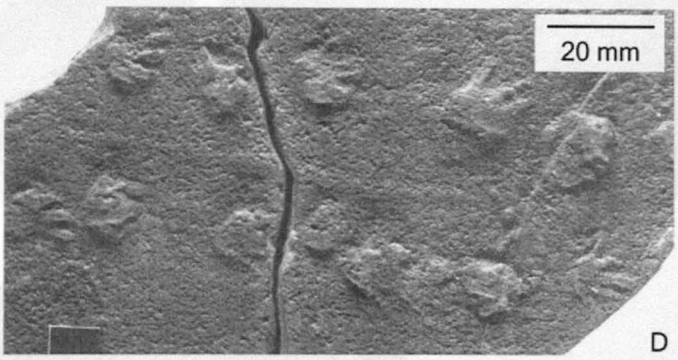
BU 3398



BU 2471



BU 3702



BU 3688

BU 3434a

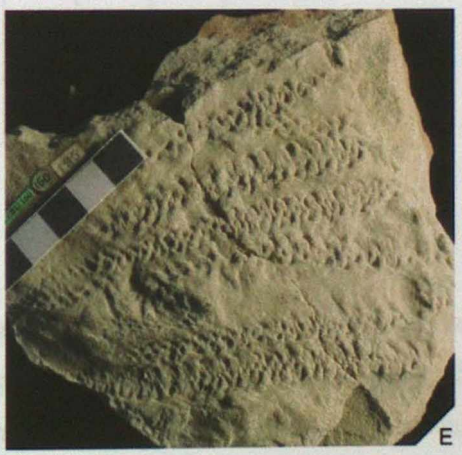
TEXT-FIG. 1.12. Vertebrate ichnotaxa present in the Alveley Member, Salop Formation, Warwickshire Group. Moscovian, Shropshire, UK. A, BU 3398, *Limnopus* (*Limnopus*) *vagus* Marsh, 1894. B, BU 2471, *Ichniotherium willsi* Haubold and Sarjeant, 1973. C, BU 3702, *Hyloidichnus? bifurcatus* Gilmore, 1927. D, BU 3688, *Limnopus* (*Batrachichnus*) Woodworth, 1900. E, BU 3434a, *Dimetropus leisnerianus* (Geinitz, 1863).

BU 4398

BU 4397

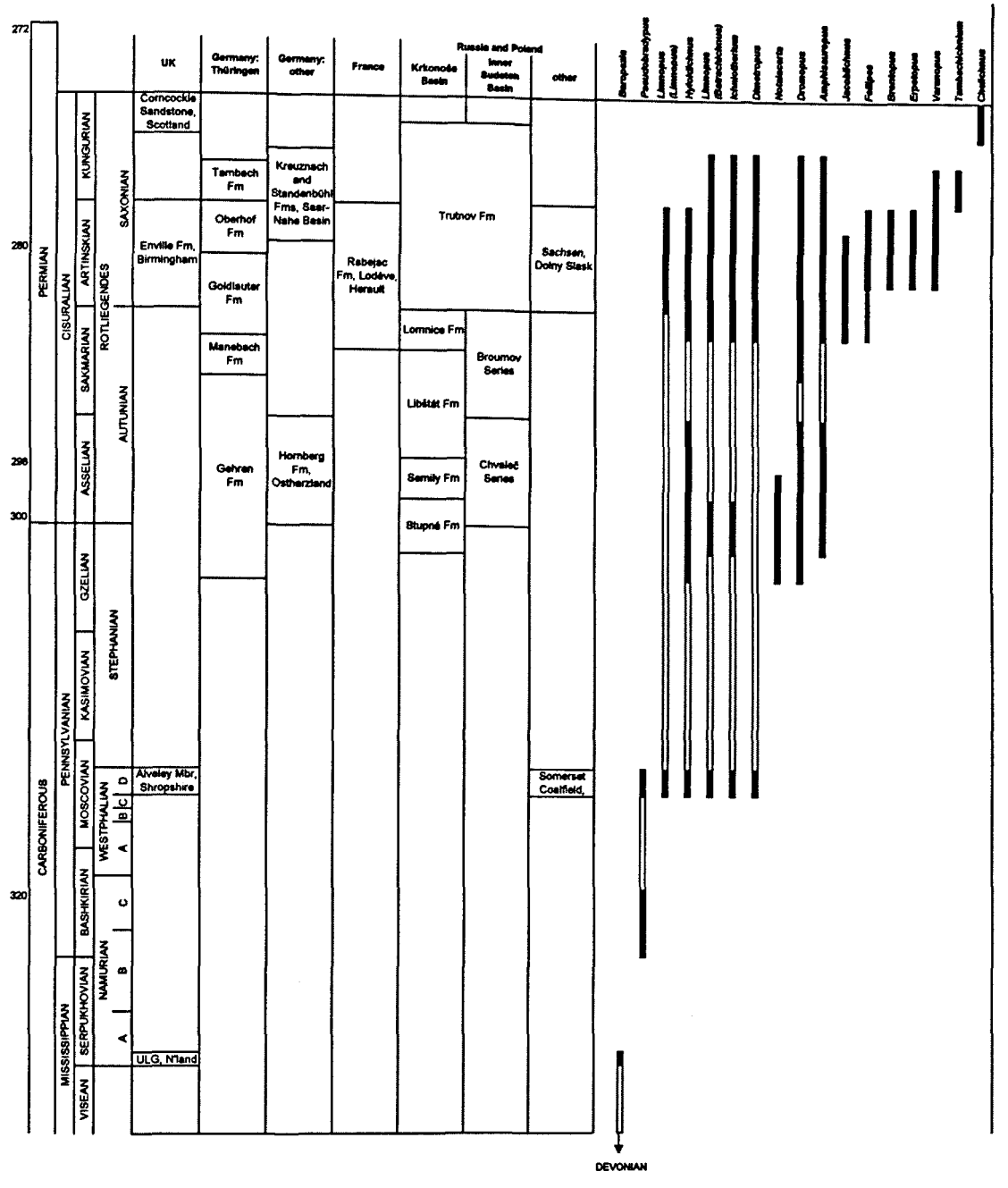
BU 159

BU 4396



BU 160

TEXT-FIG. 1.13. Vertebrate ichnotaxa and floral taxa from the Enville Member, Salop Formation, Warwickshire Group. Moscovian, Shropshire, UK. A, BU 4398, *Limnopus* (*Limnopus*) *vagus* Marsh, 1894. B, BU 4397, *Dromopus lacertoides* (Geinitz, 1861). C, BU 159, D, BU 4396, E, BU 160, *Walchia* sp.



TEXT-FIG. 1.14. Stratigraphical distribution of tetrapod ichnotaxa through the Late Carboniferous and Early Permian of Europe, illustrating the age of major trackway-bearing formations. The Alveley ichnoassemblage extends the stratigraphical ranges of a number of predominantly Permian ichnotaxa back into the mid-Late Carboniferous. Solid black lines indicate ichnotaxon appearance, white lines indicate ghost ranges, grey lines indicate uncertain ranges due to indeterminate ichnotaxon classification. Mbr, Member; Fm, Formation; Gp, Group; ULG, Upper Limestone Group; N'land, Northumberland; *L.* (*Limnopus*), *Limnopus* (*Limnopus*); *L.* (*Batrachichnus*), *Limnopus* (*Batrachichnus*). Data sources for individual columns: Boy and Fichter 1988; Clack 1997; Haubold 1971*a*, *b*, 1998, 2000; Haubold and Katzung 1975; Haubold and Stapf 1998; McKeever and Haubold 1996; Milner 1994; Scarboro and Tucker 1995; Tucker and Smith in press (Chapters 2–3).

as *Ichniotherium willsi* Haubold and Sarjeant, 1973, *Hyloidichnus? bifurcatus* Gilmore, 1927, *Dimetropus leisnerianus* (Geinitz, 1863), *Limnopus* (*Batrachichnus*) *plainvillensis*, Woodworth, 1900, *L.* (*Batrachichnus*) *salamandroides* (Geinitz, 1861), and *L.* (*Limnopus*) *vagus* Marsh, 1894 (Chapter 3). The recognized ichnotaxa represent an early marginal freshwater–terrestrial tetrapod community, developed shortly after the appearance of the amniotes during the early Westphalian (Upper Bashkirian – Lower Moscovian). The ichnofauna is characterised by a high frequency and low diversity of stem-lissamphibian tetrapods of the paraphyletic group 'Temnospondyli' (95 per cent of the trackways), as represented by the ichnogenus *Limnopus*. The ichnogenera *Dimetropus*, *Ichniotherium* and *Hyloidichnus* represent a smaller, relatively low diversity amniote assemblage (5 per cent), of inferred ophiacodontids, diadectomorphs, and varanopsids, sphenacodontids or procolophonids respectively (Chapter 4).

Hardaker (1912) was the first to report on the discovery of vertebrate trackways in the Enville Member. Six genera were recognised, and these were named according to the ichnotaxonomic nomenclature suggested by Pabst (1908). The ichnotaxa were identified as *Ichnium sphaerodactylum*, *I. pachydactylum*, *I. brachydactylum*, *I. dolichodactylum*, *I. gampsodactylum* and *I. acrodactylum*, and these names corresponded to varying modes of preservation within the trackway assemblage, rather than providing any information on trackmaker identities. In consequence, Haubold and Sarjeant (1973, 1974) revised the Enville ichno-assemblage, although they too recognised six ichnotaxa: *Anthichnium salamandroides* (Geinitz, 1861); cf. *Amphisauropus latus* Haubold, 1970; *Dromopus lacertoides* (Geinitz, 1861); *Gilmoreichnus brachydactylus* (Pabst, 1900); *Dimetropus leisnerianus*; and *Ichniotherium cottae* (Pohlig 1885). A restudy of the Enville Member confirms the presence of four of these taxa (*Limnopus* (*Batrachichnus*) *salamandroides* (formerly *A. salamandroides*), *Hyloidichnus bifurcatus* (formerly *G. brachydactylus*), *D. leisnerianus*, and *D. lacertoides*; Text-fig. 1.13). However, *I. cottae* is absent, and specimens assigned to *A. latus* are here attributed to *Limnopus* (*Limnopus*) *vagus* (Text-fig. 1.13; Chapter 3). As in the Alveley ichno-assemblage, approximately 80 per cent of the trackways represent the traces of stem-lissamphibian biotaxa, whilst the remainder represent a mixture of stem and crown-group amniotes. For example, *Dimetropus* is thought to represent an early synapsid trackmaker, such as a 'pelycosaur', whilst *Dromopus* represents an araeoscelid (Chapter 4). However, unlike the Alveley assemblage, very few small trackmakers are represented, and the material is dominated by very large *Limnopus* (*Limnopus*) trackways, which are not found at such sizes within the Alveley Member. This, together with the presence of *Dromopus*, a typically coastal or semi-arid indicator ichnotaxon, is evidence for considerably different palaeoenvironments within the Alveley and Enville Members.

The Salop material comprises typical Late Carboniferous–Early Permian red-bed ichnotaxa, as recognized by Haubold and Stapf (1998). This vertebrate ichno-assemblage extends knowledge of

Palaeozoic ichnofaunas back into the mid-Late Carboniferous, a period for which little is known regarding terrestrial tetrapod communities, in comparison with well-documented Permian and Triassic faunas. Most of the ichnogenera in this Moscovian (Westphalian D–Stephanian) assemblage are otherwise restricted to the latest Carboniferous and Permian, and the assemblage produces significant stratigraphical range extensions in the amniote and stem-lissamphibian trackway record (Text-fig. 1.14).

The relative diversity and frequency of ichnotaxa at any one site is heavily influenced by environmental factors, in particular geographical and sedimentological setting. However, no Early Permian ichno-assemblage displays such a marked dominance of temnospondyl amphibian trackways of a single ichnogenus, in conjunction with an exceptionally low diversity and number of amniote trackways, as that found within the Salop ichno-assemblages.

Invertebrates

A limited number of invertebrate trackways are preserved within the Alveley Member as moulds (concave epireliefs) upon the upper surfaces of the siltstone beds within which the vertebrate trackways were originally produced (Text-figs 1.15, 1.16). These have been identified as undertracks of *Koupichnium* Nopsca, 1923, and are thought to represent members of the Xiphosurida (Størmer 1955).

Flora

The flora of the Salop assemblages has never been considered in full, although Florin (1938–1945) figured four specimens from the Enville Member in a systematic overview of Late Palaeozoic plants; these specimens were identified as *Walchia schneideri* (BU 156), *Lebachia parviolia* (BU 157; BU 159), and *Ernestiodendron filiciforme* (BU 160). These specimens have subsequently been attributed to the conifer form genus *Walchia*. The flora of the Salop Formation as a whole is typical of Westphalian floodplain and levee assemblages as recognised by Scott (1980). Ferns, lycophytes, and sphenopsids dominate, whilst the presence of conifers implies an 'upland', extra-basinal, or arid climate influence (Mack *et al.* 1995; Rothwell *et al.* 1997; Text-fig. 1.15).

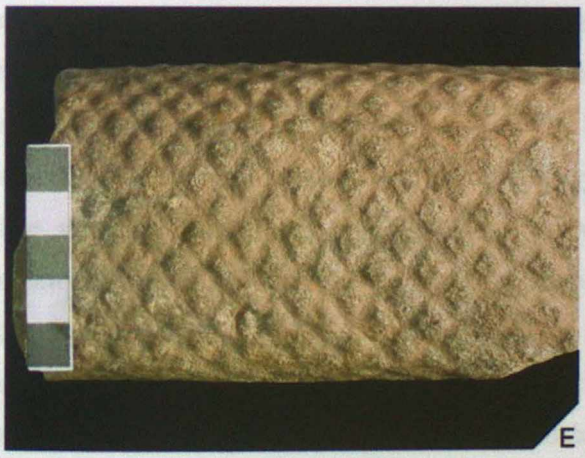
The Alveley Member contains abundant *Cordaites* sp. and also the tree-fern *Acitheca polymorpha*. This latter species is useful as an age indicator for the Alveley Member, which cannot be any younger than Moscovian (Westphalian D; Cleal pers. comm.). *Calamites suckowii* and *Lepidodendron* sp., an arborescent lycophyte, are present to a lesser extent, as is the conifer form genus *Walchia*. The Enville Member flora is similar, containing *Cordaites* sp. and *Walchia*, but differs in containing pteridosperms (*Alethopteris*) whilst lycophytes are absent.

BU 4399

BU 4402

BU 4401

BU 4400



BU 4403

BU 3727

TEXT-FIG. 1.15. Floral taxa and invertebrate ichnotaxa from the Alveley Member, Salop Formation, Warwickshire Group. Moscovian, Shropshire, UK. A, BU 4399, *Acitheca polymorpha*. B, BU 4402, *Walchia* sp.. C, BU 4401, *Calamites suckowii*. D, BU 4400, *Cordaites* sp.. E, BU 4403, *Lepidodendron* sp.. F, BU 3727, *Koupichnium* Nopsca, 1923.

Taphonomy

Vertebrate and invertebrate trackways

Sedimentary sequences comprised of alternating sand and mud horizons characteristic of fluctuating depositional rates, such as those of the Salop Formation, provide the greatest preservation potential for trackways (Thulborn 1990). Short periods of exposure enable trackways to be produced across an area of soft sediment, whilst subsequent, periodic deposition covers this horizon, forming casts of the footprints (Text-fig. 1.16). A fossil trackway therefore typically comprises two impressions, the first representing the original imprint upon the exposed surface (a mould, or concave epirelief) and the second forming a cast (or convex hyporelief) of this. The vertebrate trackways from the Salop Formation are preserved as convex hyporeliefs upon the depositional bases of fine- and medium-grained sandstone beds, whilst the invertebrate traces are found as concave epireliefs within the alternating mudstone horizons. The different mode of preservation reflects the different environments within which these trackways were formed. Vertebrates traversed the slightly coarser, exposed substrates of point bar complexes and river levees, whilst xiphosurans were aquatic (Anderson 1994), and consequently left their impressions on finer-grained sediments in shallow lacustrine or fluvial areas.

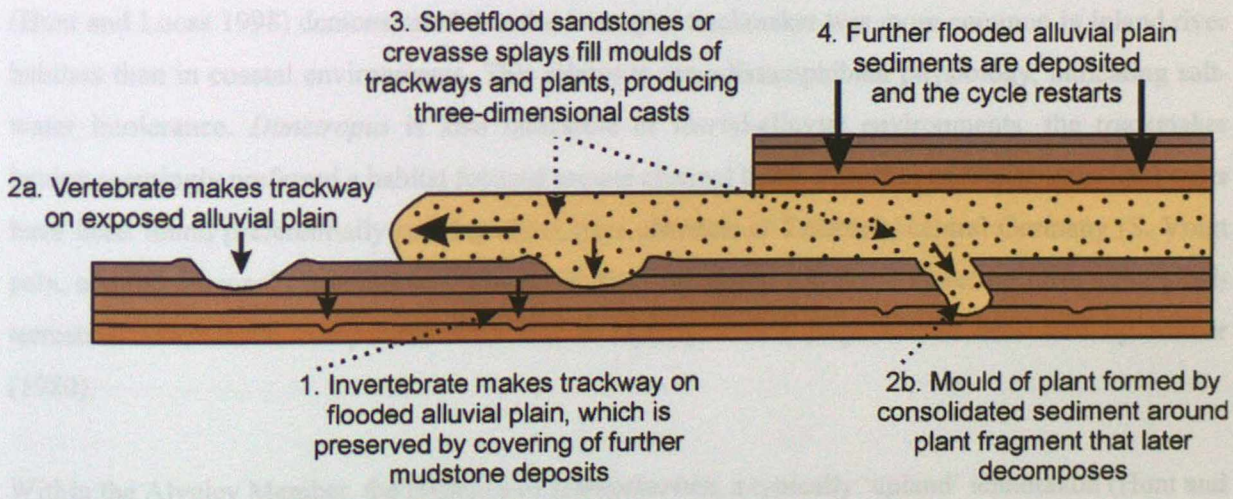
The consistency of the sedimentary horizon within which any trackways were originally made significantly affects the preservation potential of these imprints. Recent experiments (J. Milan pers. comm., S. J. Jackson pers. comm.) have demonstrated that trackways in very wet sediment merely collapse upon extraction of the foot, and form highly deformed traces. In contrast, if the sediment is too dry, no impression will be made. The sediment must possess a certain level of cohesion in order to maintain well-defined footprints (Brand 1979, 1996), and this may perhaps be achieved through a specific clay mineral composition, or binding by microbial mats. Small, millimeter-scale, *Kinneyia*-like structures are found on vertebrate trackway specimens from both the Alveley and Enville members, which may indicate the presence of microbial mats. This is also suggested by the presence of aligned micas along bedding plane surfaces, although these could equally derive from periods of standing water. Desiccation cracks often dissect vertebrate footprints within the Salop Formation, and this suggests that post-impression drying and hardening of the soft substrate further improved the resilience of trackway moulds.

The lack of body fossils within the Salop Formation (and, indeed, the Warwickshire Group as a whole) is best explained by the environment of deposition. Trackways and body fossils rarely co-occur, as their preservation is favoured by different conditions. Skeletal material is often best preserved where sedimentation occurs rapidly and in large volumes, which in turn requires large amounts of fast-moving water that would easily erode trackways. In contrast, trace fossils can withstand relatively long periods of exposure (Thulborn 1990) that would greatly decrease the preservation potential of skeletal

material. The alternating periods of exposure and deposition characteristic of the trace fossil bearing Salop Formation are also typified by associated sedimentary structures such as raindrop imprints, desiccation cracks, ripple lamination, and palaeosol horizons.

Flora

Modes of preservation within plant fossils vary according to the degree of compression that has occurred during early burial and diagenesis, and the composition of any organic components that may remain (Spicer 1989; Cleal and Thomas 1994). Plants within the Salop Formation exhibit two distinctive preservational states. Firstly, *Walchia* specimens show a typical mode of impression preservation for conifers, having been draped with a thin mud cover before final deposition and burial (Kerp pers. comm.). In contrast, the remaining taxa (*Acitheca*, *Calamites*, *Cordaites*, *Lepidodendron*, *Alethopteris*) are preserved as three-dimensional, inorganic casts. These are typical of plants such as *Calamites*, where the stem comprised an outer woody layer and a delicate, easily degradable, pithy core during life (Cleal and Thomas 1994). Following burial, lithifying sediment creates a mould around the resistant plant fragment, providing that consolidation occurs before the fragment is crushed (Taylor 1981). Subsequent decomposition of the organic plant material leaves a cavity that may later be infilled, producing a cast of the original specimen (Taylor 1981; Cleal and Thomas 1994); however, little or no organic matter remains.



TEXT-FIG. 1.16. A depositional cycle of periodical flooding and exposure across an alluvial plain is the optimal sedimentological environment for the preservation of trackways and floral casts.

Ecosystems of the Salop Formation

The Moscovian assemblage from the Salop Formation offers a unique insight into Late Carboniferous palaeocommunities. Although key body fossil localities (such as Nýřany, Czech Republic; Joggins and Florence, Nova Scotia; Fort Sill, Oklahoma; Linton, Ohio and Mazon Creek, Illinois) have greatly increased our knowledge of Late Carboniferous and Early Permian assemblages and associations (e.g. Fritsch 1883; Romer 1930; Steen 1938; Gregory 1950; Olson 1951, 1967; Carroll 1966, 1967; Reisz 1975; Nitecki 1979; Milner 1980, 1987; Baird *et al.* 1985; Hook and Ferm 1985), data from the Salop Formation occur mainly in the form of entirely autochthonous trace fossil material. In consequence, this enables the examination of communities in areas that do not normally preserve body fossils, and may either support or contradict interpretations based upon data provided by skeletal material. Additionally, trace fossil material provides information on aspects not offered by skeletal material including, for example, the preferred habitats, or ecological niches of various taxa, and taxon interactions.

Vertebrates

Vertebrates represented by trackways in the Salop Formation comprise a combination of primitive, amphibious forms (stem-lissamphibians, or 'temnospondyls') and more derived, amniote taxa (diadectomorphs, ophiacodontids, and araeoscelids, varanopsids, sphenacodontids or procolophonids). The vertebrate ichno-assemblage is dominated by trackways of the ichnogenus *Limnopus*, which can be correlated with stem-lissamphibian trackmakers (Chapter 4). A study of the distribution of *Limnopus* along a transect through coastal, fluvial-alluvial and 'upland' environments in New Mexico (Hunt and Lucas 1998) demonstrated that the *Limnopus* trackmaker was more common in inland river habitats than in coastal environments. This relates to stem-lissamphibian physiology, indicating salt-water intolerance. *Dimetropus* is also indicative of fluvial-alluvial environments, the trackmaker having seemingly preferred a habitat focused around channel belts; a number of *Dimetropus* trackways have been found preferentially running along river channels at Tambach, central Germany (S. Voigt pers. comm., personal observations). The majority of the Salop ichnotaxa therefore form a marginal-terrestrial association, comparable with that at Nýřany, Czech Republic, as described by Milner (1980).

Within the Alveley Member, the presence of *Ichniotherium*, a typically 'upland' ichnotaxon (Hunt and Lucas 1998; Voigt and Haubold 2000) suggests a more terrestrial aspect to the community at this stage. This correlates with the interpretation of *Ichniotherium* as a diadectomorph trackway (Chapter 4), as these herbivorous forms appear in the fossil record in conjunction with typically 'upland' Carboniferous floras (Milner 1980; Scott 1980). Even so, ichnotaxa associated with more arid environments (*Dromopus*, *Chelichnus*) are absent from the Alveley assemblage. In comparison, within the Enville Member, *Ichniotherium* is absent and *Dromopus* is present. This may indicate the changing

climate of the latest Carboniferous towards increasing aridity, but *Dromopus* is only present as a single footprint, and this is not enough to provide conclusive evidence. The absence of *Ichniotherium*, which is only present as a single trackway in the Alveley Member, may be artefactual, given the small sample size of the Enville assemblage. Alternatively, it may indicate the absence of diadectomorphs within the slightly drier, unstable environment represented by the Enville Member. It is possible that this environmental instability accounts for the presence of large amphibious forms (represented by *Limnopus* (*Limnopus*)) within the Enville Member, whilst such forms are absent from the Alveley assemblage. Perhaps smaller, juvenile stem-lissamphibians were more reliant upon a constant water source than their adult contemporaries. The frequent flood events and drier floodplains of the Enville Member would therefore render this habitat less preferable to smaller amphibians than larger forms, which may have been able to venture farther from water when not breeding. A segregation of adult and terrestrial juvenile stem-lissamphibians may therefore have occurred, with the smaller forms inhabiting the wet floodplains of the Alveley Member, and the adults preferring a slightly drier habitat, as represented by the Enville Member. An alternative explanation would be that the difference in average size of *Limnopus* trackways within the Alveley and Enville members is a reflection of different biotaxonomic groups present within these two environments, rather than an indication of the average age of each tetrapod community. These hypotheses cannot be tested, as the trackways of a number of stem-lissamphibian genera are indistinguishable (Chapter 4).

Invertebrates

Only one group of invertebrates, the Xiphosurida, is represented in low abundance by trackways (*Koupichnium*) in the Alveley Member (Text-fig. 1.15). This may be a preservational artefact rather than a representative sample, as these small invertebrate trackways are found only within the very thin, fine-grained mudstone horizons that directly overlie the sandstone beds containing the vertebrate trackways. These horizons deconsolidate preferentially upon collection, and fewer invertebrate trackways are discovered in consequence. It has been suggested that xiphosurans inhabited aqueous environments within continental settings (Størmer 1955; Anderson 1994), and the presence of *Koupichnium* therefore indicates that at stages during the deposition of the Alveley Member, the floodplain area was either completely inundated by water, or contained shallow, ephemeral lakes and streams.

Flora

The floral component of any fossil assemblage does not necessarily represent the local plant population. Few plant fossils are found *in situ* (Scott 1980; Cleal and Thomas 1994), and the composition of most assemblages is largely controlled by the interaction of the floral ecology with the sedimentary environment and dominant depositional processes acting within it (Scott 1980), rather than the true composition of the local floral population. The majority of plant remains are found as

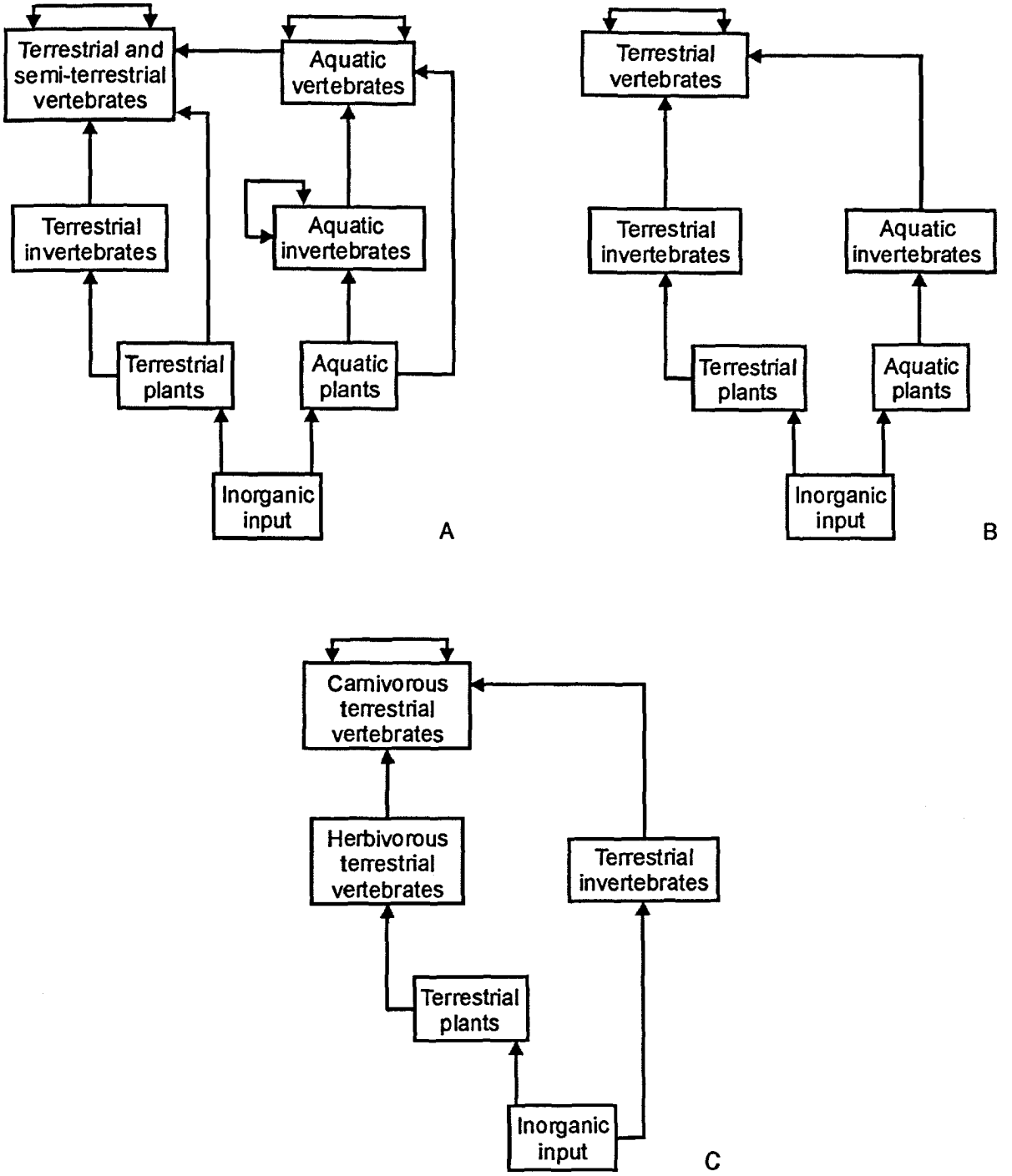
fragments that have often been transported over large distances after natural detachment (abscission) or traumatic removal from the parent plant (Cleal and Thomas 1994). These factors must be considered when interpreting the palaeoecology and palaeoenvironment of most localities at which plants are preserved.

The floral assemblage from the Salop Formation reflects the influence of a mixture of lowland (fluvial-alluvial) and 'upland' (extra-basinal) environments, as indicated by the vertebrate ichnotaxa. Marattialean tree ferns, such as *Acitheca*, indicate a floodplain environment (Cleal and Thomas 1994), although *Walchia* conifers were adapted for growth in dry soils in arid, moisture-stressed habitats (Rothwell *et al.* 1997). A drying trend is evident through the Alveley and Enville members, indicated by their component floras. The Alveley Member contains lycophytes, which are characteristic of clastic swamp or lowland peat environments (Cleal and Thomas 1994), whilst *Calamites* serves as a humid-wet environment indicator, having often occurred in monotypic stands along lake and river shorelines in wetland soils (Gastaldo 1987). These typically wetland plants are absent within the Enville Member, however, which instead contains pteridosperms (*Alethopteris*), indicators of dry conditions within a floodplain setting (DiMichele *et al.* 2001). In terms of its use as an environmental indicator, *Cordaites*, which comprises the bulk of the specimens within both the Alveley and Enville Members, was ecologically diverse, occupying a wide range of habitats both wet and dry (Cleal and Thomas 1994). End-Carboniferous climate change caused the general movement of typically 'upland' floras to more lowland areas, coupled with a change in the dominant forms from lycophytes to marattialean tree ferns (Scott 1980; DiMichele *et al.* 2001; DiMichele and Phillips 2002), and this trend is evident within the Salop assemblages.

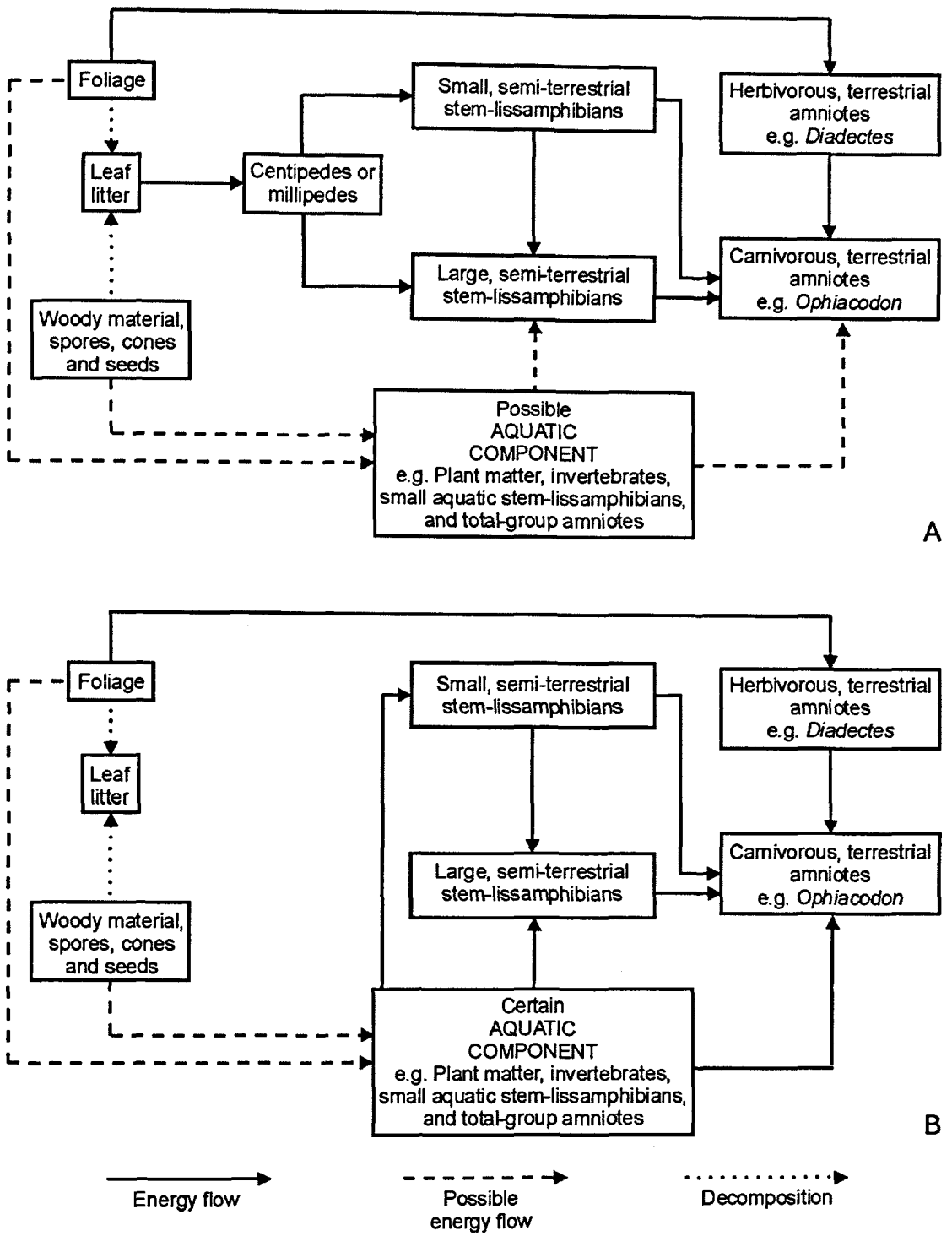
Biotic interactions

Olson (1971) presented three hypothetical trophic structures to describe interactions between the terrestrial components of Late Palaeozoic vertebrate communities (Text-fig. 1.17). The community structure of the Salop assemblage seems to be most similar to Olson's model 'C' (Olson 1971, fig. 155C, p. 650; Text-fig. 1.17C), where the trophic structure relies mainly on herbivorous terrestrial vertebrates feeding on terrestrial plants, and the trophic chain ends with terrestrial carnivorous vertebrates feeding upon their herbivorous contemporaries. Trophic interaction between terrestrial invertebrates, plants and carnivorous vertebrates occurs, but to a less significant degree. However, this model implies that the terrestrial community is isolated from any aquatic component, and although there is no evidence for an aquatic community sector in the Salop assemblage, this is may be a preservational artefact. It is likely that aquatic flora and fauna formed part of the trophic structure – which would instead resemble Olson's model 'A' (Olson 1971, fig. 115A, p. 650; Text-fig. 1.17A) – however the extent to which interaction occurred is impossible to judge. Consequently, two models are suggested for trophic structure within the Salop assemblage. The first (Text-fig. 1.18A) assumes that

the majority of trophic exchange occurs within the terrestrial environment, with the possible presence of an interacting aquatic component, whilst the second (Text-fig. 1.18B) postulates that trophic exchange relies upon the presence of an aquatic sector of the population that forms the base of the trophic structure. The components of the trophic system within the Alveley and Enville members are the same, but the system varies in the proportion of these components and the level of interaction between them.



TEXT-FIG. 1.17. Three types of structure for terrestrial vertebrate communities. A, the majority of trophic exchange occurs through the aquatic component of the fauna, with the base of the trophic structure dependent on aquatic plants. B, the trophic structure is dependent upon exchange through terrestrial invertebrates. C, the main exchange occurs through herbivorous, terrestrial vertebrates. Adapted from Olson (1971).



TEXT-FIG. 1.18. Postulated trophic structures within the Salop Formation community. A, The majority of exchange occurs between terrestrial components of the fauna, whilst a possible aquatic component (not represented within the Salop assemblage) interacts to an unknown degree. This model assumes the presence of terrestrial invertebrates (millipedes or centipedes), although there is no evidence of these in the Salop Formation. B, Most of the exchange occurs within a highly influential aquatic component of the fauna, on which the terrestrial components are heavily reliant. Data for trophic links from Milner (1980), Olson (1971), Reisz (1986), Scott (1980), and Scott *et al.* (1992).

Summary

1) The Moscovian (Westphalian D) assemblages of the Salop Formation are the only comprehensive vertebrate trace fossil assemblages of Late Carboniferous age in Europe, and together with invertebrate and plant data, provide a unique insight into Late Carboniferous terrestrial communities.

2) The Alveley Member represents a braided river environment, within a wet floodplain setting. This is reflected by the abundance of small, water-reliant stem-lissamphibians (represented by the ichnogenus *Limnopus*), and the presence of lycophytes, *Calamites*, and the marattialean tree fern *Acitheca*. The ichnotaxon *Ichniotherium* (representative of diadectomorphs) and *Walchia* indicate a minor 'upland' or arid-climate influence.

3) The Enville Member represents a drier floodplain environment that was exposed for longer periods, reflecting the drying trend through the Late Carboniferous. This trend reflects climate change towards increasing aridity. *Dromopus*, an ichnotaxon often used as an arid climate indicator, appears in the Enville Member and although stem-lissamphibians still dominate, smaller/juvenile forms are less common. The flora changes from taxa suggestive of wet floodplain environments to those typical of dry floodplain habitats (pteridosperms, *Walchia*).

4) The Salop assemblages do not preserve aquatic fauna and flora, but it is hypothesized that an aquatic component may have been present and contributed to the trophic structure, forming the base of the food web. Other important mechanisms of energy transfer through the terrestrial trophic structure relied on carnivory amongst stem-lissamphibians, and terrestrial herbivorous tetrapods feeding upon terrestrial plants.

5) The presence of the fern *Acitheca polymorpha* indicates that the Alveley Member can be no older than Moscovian (Cleal pers. comm.), a detail that supports Besly and Cleal (1997) and McNestry's (1994) palaeobotanical and palynological dating.

6) In conclusion, the Salop Formation illustrates the transition from wet, humid Late Carboniferous environments, dominated by stem-lissamphibians and lycophytes, to Early Permian communities comprising mainly amniotes, conifers, and marattialean tree ferns within a semi-arid setting.

CHAPTER 2

VERTEBRATE ICHNOSPECIES CONCEPTS AND NUMERICAL TAXONOMY

Vertebrate trackways are not biological forms, capable of evolution and divergence, but inorganic units created by a synthesis of an organism with its environment. Although a biological form is represented, albeit indirectly, other factors such as substrate conditions or trackmaker behaviour may strongly influence trackway formation. One biological form is capable of making more than one type of trace, and one type of trace can often be produced by a number of different biological taxa; trace fossils are not attributable to 'species' in the purely biological sense, as recent organisms are, or even to 'morphospecies' at the same level as body fossils. Consequently, trackways cannot be used to reconstruct phylogenies, nor to determine evolutionary patterns and processes. The main aim in classifying trace fossils, therefore, is to enable stability and conformity in description, and to allow methodical studies (Bromley 1996), rather than to extract a hypothesis of evolutionary relationships. Ichnotaxa are significantly different from biotaxa in this sense, and different species concepts should be applied in compiling the two taxonomical classifications.

Phylogenetic methods, and hence phylogenetically derived taxonomical classifications, operate by distinguishing similarities based upon common ancestry, and require conjecture upon evolutionary directions, inferring the pattern of branching groups. As discussed above, trackways may represent more than one biotaxon, and one biotaxon may produce more than one type of trackway. Consequently, trackways as single, inorganic entities cannot be said to have a 'common ancestry' in the biological sense. Whilst vertebrate trackways represent their trackmaker to an extent, the number of other factors influencing trackway morphology is so large that 'ancestors', and 'monophyletic groups' based purely upon morphological differences between traces would not form 'natural units', representing evolutionary relationships, but artificial groups based upon preservational artefacts caused by superficial alterations in the conditions under which the traces were produced. Thus, if phylogenetic methods were used to classify trackways, the resulting phylogeny would be misleading; it would not reflect the true phylogenetic relationships of the trackmakers themselves. In any case, attempting to reconstruct phylogenies based upon inorganic units, which do not evolve as biological taxa do, is inappropriate.

Trackway classification is therefore better accomplished with the use of purely phenetic methods. These do not aim to provide an outline of evolutionary relationships, as phylogenetic methods do, but instead enable taxa, or units, to be grouped and distinguished based upon their morphological characteristics. Phenetic methods produce a hierarchical classification similar to the Linnaean taxonomic system, based upon the degree of *difference* between the taxonomic units, rather than upon *shared* characteristics, as in phylogenetic analysis. In order to provide some correspondence with

trackmaker phylogenies and biological species, it is best that trackways be classified using only those characters directly related to trackmaker anatomy, and not extra-morphological features created by substrate consistency or trackmaker behaviour (Tucker and Smith in press). However, this view is challenged by the taxonomic methods of some authors (for example, Fichter 1982, 1983*a*, *b*, *c*, 1984, 1994). The methods of authors such as Haubold (1998), Voigt (2001), and Tucker and Smith (in press), are supported here, for reasons explained below.

The present state of vertebrate ichnotaxonomy

At present, there appear to be two philosophies regarding the construction of vertebrate ichnotaxonomy:

1. Trackway taxonomy can be based upon the detailed morphological variation within trackways, including extra-morphological characteristics created by differences in substrate conditions rather than only trackmaker anatomy. Such classifications have been compiled by, for example, Fichter (1982, 1983*a*, *b*, *c*, 1984, 1994), Schmidt (1959), and Gilmore (1926, 1927, 1928). This method identifies trackways to a highly descriptive level, and differentiates between trackways created by the same organism exhibiting different types of behaviour (for example, running, walking and swimming). This taxonomic procedure closely matches that used by invertebrate ichnologists (Bromley 1996).

2. Trackway taxonomy can be based purely upon inferences of trackmaker identity, utilising only those features that relate directly to trackmaker anatomy for diagnosis and identification. Such classifications can be observed in the work of Haubold and associates (e.g. 1998, 2001; Haubold and Lucas 2001; McKeever and Haubold 1996; Haubold and Stapf 1998), Voigt (2001). Tucker and Smith (in press), also adopted this method, and stated that trackways should be classified using only well-preserved, surface level traces, and the results used to classify less well-preserved material, following the extensive study of trackway variants. This taxonomy seeks to enable an easier combination of trackway and body fossil data, allowing the two different types of preservation to yield distinct, yet comparable information.

Whilst the first method of compiling ichnotaxonomic classifications may divulge some information regarding substrate or trackmaker ethology at the time of impression, this technique leads to a high level of taxonomic splitting (Farlow and Pianka 2000). Several ichnogenera may incorporate the trackways of only a single taxon of trackmaker. The resulting ichnotaxonomy consequently implies an artificially high diversity of biological forms, and does little to advance our knowledge of trackmaker communities and ecology. This problem is overcome with the use of the second method, which aims to correlate trackmaker and trackway taxonomy to the greatest possible extent, and is thus more advantageous. The more closely the two classifications can be matched, the greater the value of

ichnotaxonomy in comparing trace fossils with skeletal material. Hence, substrate and ethologically-influenced variants should be accepted as inter-ichnospecific variation and included within ichnospecific descriptions. It is, nevertheless, highly unlikely that trackway taxonomy exactly mirrors body fossil taxonomy, and the next consideration is the hierarchical level to which the two can in fact be correlated.

Operational and theoretical aspects of a typological ichnospecies concept

An effective taxonomy, whether biological or ichnological, should not only enable the classification of objects for scientific study and to facilitate specimen recognition, it should also be predictive. In other words, it should allow deductions to be made about a taxon, based upon its placing with other taxa sharing similar characteristics within higher level taxonomical groups. In biological taxonomy, a phylogenetic species concept is consistent with this, as the taxonomic groupings are based upon synapomorphies, which are, by definition, shared characteristics. However, a morphological, ichnological species concept relies upon the phenetic organisation of trace fossils into 'natural groups' in the Aristotelian sense. These are 'classes of objects, members of which share certain defining properties', and are considered the most informative of all possible taxonomic groupings, with a higher likelihood of engendering accurate predictions (Gilmour 1937; Sneath and Sokal 1973). Problems arise, however, in selecting these 'defining properties'. Subjectivity is introduced in deciding which characters are significant, and to what taxonomic level these characters can be applied. What, for example, distinguishes a specific character from a generic character? This question can only be answered following comprehensive study of the taxon or group of taxa under consideration, and depends upon the nature of the group, and the variation within specimens. Nevertheless, these decisions remain somewhat subjective. In order to reduce bias in ichnotaxonomy, it is suggested that numerical methods provide the most appropriate, objective classifications. Numerical taxonomy also benefits from being based upon stable, repeatable evidence.

NUMERICAL TAXONOMY AND STATISTICAL ANALYSIS OF *LIMNOPUS*

95 per cent of the Alveley ichno-assemblage comprises trackways hitherto assigned to the ichnogenera *Limnopus* Marsh, 1894, *Batrachichnus* Woodworth, 1900 and *Anthichnium* Nopsca, 1923, of which 66 per cent are exceptionally well-preserved, surface-level traces. These trackways afford an opportunity to examine ichnospecific diversity and morphological variation within this assemblage using multivariate techniques (Tucker and Smith in press). The ichnotaxonomy of the assemblage is stabilised using numerical analysis, as advocated above. Specimens from the Enville Member do not form continuous trackways, and so are not appropriate for detailed numerical analysis. Only one ichnotaxon, *Dromopus lacertoides*, is present in the Enville Member but absent in the Alveley Member, and as this only represented by a single, poorly preserved footprint, and the author has nothing to add taxonomically, it is not further considered. For a full systematic review of *Dromopus* see Haubold (1971*a*).

Numerical taxonomy

Numerical taxonomy in this context can be defined as the classification of taxonomic units into taxa based upon the numerical analysis of a number of pre-defined characters and character states. The concepts upon which this definition is based trace back to the French botanist Michel Adanson (1727–1806) and are hence termed 'neo-Adansonian', as reviewed by Sneath and Sokal (1973, p. 5). These principles are:

1. The greater the content of information in the taxa of a classification and the more characters on which it is based, the better a given classification will be.
2. *A priori*, every character is of equal weight in creating natural taxa.
3. Overall similarity between any two entities is a function of their individual similarities in each of the many characters in which they are being compared.
4. Distinct taxa can be recognized because correlations of characters differ in the groups of organisms under study.
5. Taxonomy is viewed and practiced as an empirical science.
6. Classifications are based on phenetic similarity.

Numerical methods were applied to the large number of exceptionally well-preserved trackways noted above (Appendix 1) in order to determine ichnotaxonomic divisions present in the Alveley ichno-assemblage. The principal method employed utilizes data from an undescribed or problematic vertebrate ichno-assemblage and evaluates the phenetic (morphological) similarity of the trackways using multivariate cluster analysis. The resulting phenogram splits the trackway 'data cases' (each case associated with a single manus–pes set), or the 'trackway mean' values (the mean value of the sum of the data cases of a single trackway) into morphologically distinguishable groups, which may then be assigned to ichnospecies or ichnogenus level by comparison with type material. This technique

provides an objective and repeatable basis for the identification and classification of further trackways into established ichnotaxa, thereby stabilizing the ichnotaxonomy, whilst giving an accurate, functional picture of ichnospecies diversity.

Whilst ternary analyses and bivariate plots *sensu* Weems (1990) show a degree of clustering within the dataset used in this study, the level of cluster overlapping was such that bivariate and ternary plots alone could not be accurately used for reliable ichnotaxa classification. However, as increasing numbers of variables (characters) were considered, clusters became more discrete. Multivariate clustering enables a potentially infinite number of variables to be included in the analysis and thereby provides a more accurate basis for ichnotaxon differentiation and classification. The successful use of multivariate cluster analysis in distinguishing vertebrate ichnotaxa demonstrates that their description should be based upon as many characters as possible, with ichnogenera defined by a unique set of diagnostic characters, backed up with a comprehensive description of all other variables.

In order for the analysis to be successful, the trackway material should be studied in detail before analyses are attempted. It is important that only established type and exceptionally well-preserved specimens from surface level trackways are used for the stabilisation of vertebrate ichnotaxonomy. In order for ichnodiversity to reflect biodiversity rather than sediment mechanics, those trackway characters known to represent merely extra-morphological features – features that are not directly preserved due to the anatomy of the trackmaker – should be excluded from the initial multivariate analysis (see Appendix 2). Once the taxonomy of the groups under study has been resolved, less well-preserved trackways can be identified with the use of the revised ichnotaxon diagnoses and with direct comparison to type material.

It should be noted that these phenetic methodologies do not aim to produce an outline of evolutionary relationships between taxa, for which phylogenetic analysis is the appropriate tool, but do provide a method for grouping and distinguishing taxa dependent upon their morphological characteristics.

Previous use of numerical methods

Numerical methods have been used previously to aid discrimination between tridactyl dinosaur footprints and trackways (Demathieu 1990; Weems 1990). Approaches involved the use of numerical parameters and mean character value ratios to explore the morphological variability within trackways, with the aim of estimating biological species diversity (Weems 1990) and to aid identification of poorly preserved footprint specimens by comparison with a well-preserved ichno-assemblage (Demathieu 1990). Moratalla *et al.* (1988) used bivariate plots, Factor Analysis and Discriminant Analysis, to successfully distinguish ornithopod and theropod trackways, whilst Farlow and Lockley (1993) employed osteometric ratios from a range of bipedal dinosaurs in comparison with equivalent

footprint measurements, in order to match tracks to trackmakers. A number of authors (e.g. Haubold 1970, 1973; Conti *et al.* 1977; Fichter 1994, 1998) have used direct numerical values taken from the trackway specimens, in conjunction with calculated figures of glenoacetabular length, forelimb length and hindlimb length to aid identification of Early Permian ichnological material. Conti *et al.* (1977) utilized data from single ichnotaxa to yield bivariate biometric analyses, exploring the variation within those ichnotaxa. However, analyses at a level higher than bivariate, examining the relationships between separate ichnotaxa, have never before been undertaken on vertebrate trackways.

Analysis of the Alveley ichno-assemblage

Firstly, all material (68 well-preserved surface-level *Limnopus*, *Batrachichnus* and *Anthichnium* trackways) was sorted *a priori* into ichnotaxa, based upon major morphological variations. The material, including other, less well-preserved specimens, was also sketched and described in order to increase familiarisation with the range of variance amongst specimens. An exhaustive list of both quantitative and qualitative characters was compiled, with which to numerically describe and analyse each well-preserved trackway (consisting of a number of trackway data cases) for taxonomic classification (see Appendix 2). The chosen variables aimed to reflect all possible features of each individual footprint, and of each trackway as a whole. Characters that describe both morphological and extra-morphological features were recorded, in order to determine variation within ichnotaxa, and only those characters directly affected by trackmaker morphology were used for multivariate cluster analysis. Quantitative measurements were made to the nearest millimetre or degree, with an error of no greater than ± 1 millimetre/degree, whilst qualitative measurements used binary notations e.g. Tail trace absent (0), present (1) (see Appendix 2). Any appropriate alterations to the original *a priori* sorting were subsequently based upon all available data, following cluster analysis.

Among the measured specimens, only those that recorded a value for every character were suitable for use in the multivariate analyses. Those specimens that could not be included in the analyses were identified afterwards by the comparison of their recorded characters with those describing the pre-identified ichnotaxa. Within the trackway dataset, some measurements were unobtainable, for example, due to obscured or poorly preserved footprints or absent prints (beyond the margin of the measured slab). This reduced the number of trackway data cases for which the data set is complete and, in order to utilize as much of the trackway data as possible, the initial cluster analyses were run using the mean values, or 'trackway mean', for each quantitative variable within each trackway. This use of means was additionally useful as the number of cases was particularly high (up to 1000 data cases), and a reduction provided a more manageable phenogram. In addition, trackways that were not made at original surface level (i.e. not 'true' ichnotaxa, but undertracks and overtracks) were omitted from the initial analyses. This ensured that only surface level trackways were used in the stabilisation of the ichnotaxonomy of the assemblage, and consequently increased the resolution of this analysis by

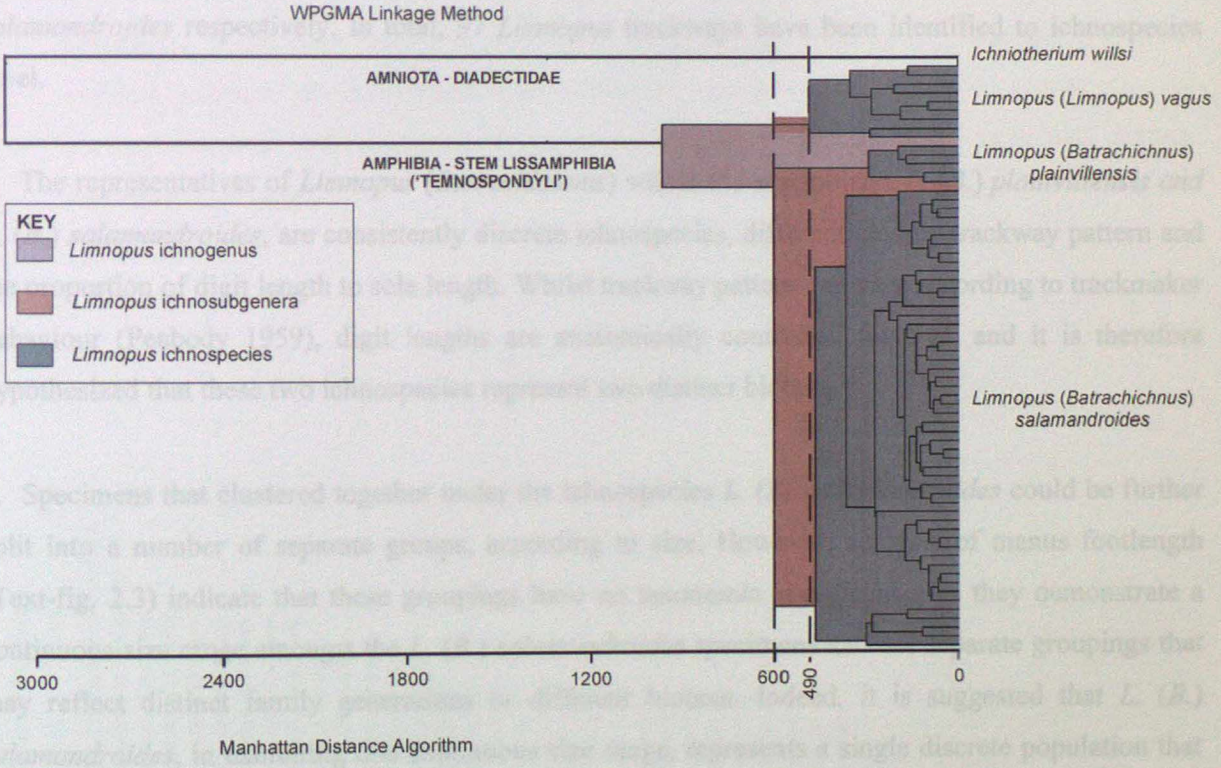
eliminating taxa that cannot be resolved as 'true' ichnotaxa. Separate analyses were run to help resolve the ichnotaxonomy of these specimens once the surface level ichnotaxonomy had been resolved. Measurements from a single trackway of *Ichniotherium willsi* were used to provide an 'outgroup' ichnotaxon.

The data were subjected to phenetic multivariate cluster analysis within *MVSP* (*Multi Variate Statistical Package*, Kovach 1999), using a number of different linkage methods and distance algorithms. These repeatedly demonstrate that the clusters found within each phenogram remain consistent throughout various combinations, indicating a high level of stability within the clustering. In the descriptions and figures below, which illustrate the results useful in resolving the ichnotaxonomy of the 'true', surface level trackways, the distance algorithm used is the Manhattan, or city-block, metric. The Sequential Agglomerative Hierarchical Nonoverlapping (SAHN) clustering linkage method used is the Weighted Pair-Group Method using Arithmetic averages, or WPGMA (Sneath and Sokal 1973; Abbott *et al.* 1985; Kovach 1999). Sixty-eight of the best-preserved surface level specimens were analysed, and, using 54 characters, a phenetic dendrogram (phenogram) was produced (Text-fig. 2.1), in conjunction with a distance matrix and a clustering report. For comprehensive reviews of the use of various multivariate clustering methods the reader is referred to Sneath and Sokal (1973), Dunn and Everitt (1982) and Abbott *et al.* (1985).

Each of the clusters were defined in conjunction with continual comparisons with the trackway material and constant referral back to the original data set, and the trackways were named by reference to the type specimens as described in the literature (Geinitz 1861; Butts 1891; Woodworth 1900; Nopsca 1923; Gilmore 1927; Baird 1952; Haubold 1970, 1971*a*, 1973; Haubold *et al.* 1995; Schult 1996), and by comparison with the type specimen of *Batrachichnus plainvillensis*. Where trackway dimensions of the type specimens had been given by these authors (e.g. Woodworth 1900; Haubold 1970, 1973), the measurements were included in a separate cluster analysis, run using only these selected characters.

Further cluster analyses were then run in order to explore the trends within the data, and to aid identification of the remaining specimens. Characters reflecting size were omitted from the analysis, and this demonstrated that although ichnotaxa are indeed based heavily upon size, some ichnotaxa are distinguishable based upon shape differences, and Principal Components Analysis confirmed this. In order to identify the trackways with indistinctly preserved digits, characters related to the digits were also omitted; this enabled the identification of a further 29 specimens. Multivariate analyses additionally gave an indication of the ichnotaxa to which undertrack specimens could be attributed, lending support to *a priori* identifications. As a consequence of these multivariate cluster analyses, the

diagnoses of the amphibian ichnotaxa found in the Alveley ichno-assemblage have been revised, and partial trackways not included in the phenetic cluster analysis have been identified accordingly.



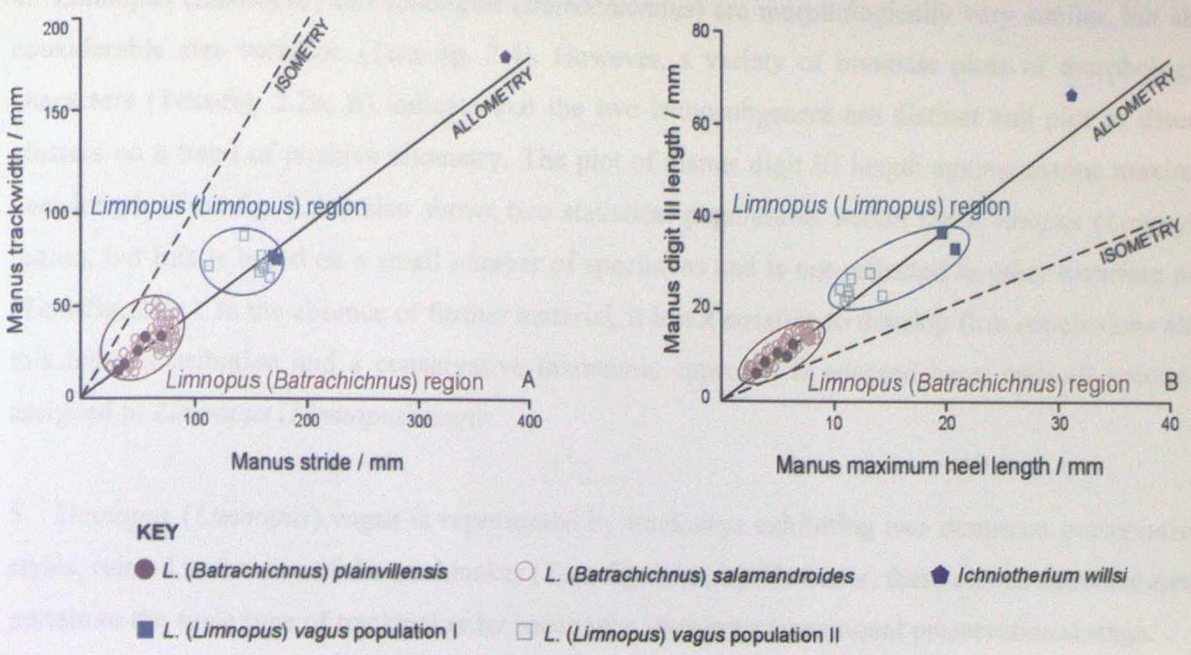
TEXT-FIG. 2.1. Phenogram illustrating results of a multivariate cluster analysis carried out upon 68 well-preserved *Limnopus* trackways, with a single specimen of *Ichniotherium willsi* as an 'outgroup' ichnotaxon.

Results

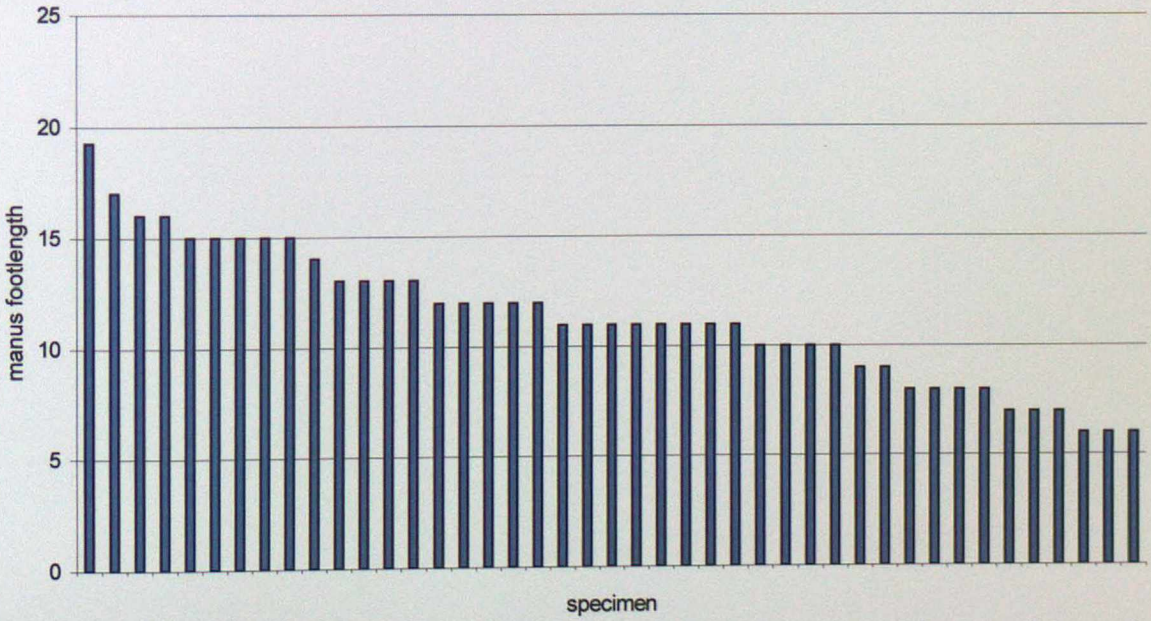
1. Following the multivariate cluster analysis of 68 well-preserved surface level trackways previously attributed to the ichnogenera *Limnopus*, *Batrachichnus* and *Anthichnium*, three ichnospecies are recognised that fall into two distinct size groupings (Text-fig. 2.2). In the interests of taxonomic resolution and stability, and because they have a slightly different stratigraphic ranges, the well-established ichnogeneric names *Limnopus* and *Batrachichnus* are retained. The ichnotaxon *Anthichnium* is interpreted as a junior synonym of the latter ichnogenus (see below). However, as no clear, morphologically based, diagnostic boundary can be drawn between *Limnopus* and *Batrachichnus*, and they differ only in terms of size, it is proposed that the two ichnogenera should be reduced to ichnosubgeneric rank under the senior available name *Limnopus*. In consequence, the 'amphibian' ichnospecies within the Alveley assemblage have been identified as *Limnopus* (*Limnopus*) *vagus* (20 specimens), *L.* (*Batrachichnus*) *salamandroides* (157 specimens) and *L.* (*B.*) *plainvillensis* (26 specimens). The ichnospecies *Limnopus rawi*, *Batrachichnus alveleyensis* and *Anthichnium major*, erected by Haubold and Sarjeant (1973, 1974), are considered to be junior synonyms of the ichnospecies *Limnopus* (*L.*) *vagus*, *Limnopus* (*B.*) *plainvillensis* and *Limnopus* (*B.*) *salamandroides* respectively. In total, 97 *Limnopus* trackways have been identified to ichnospecies level.

2. The representatives of *Limnopus* (*Batrachichnus*) within the assemblage, *L.* (*B.*) *plainvillensis and L.* (*B.*) *salamandroides*, are consistently discrete ichnospecies, differentiated by trackway pattern and the proportion of digit length to sole length. Whilst trackway pattern can vary according to trackmaker behaviour (Peabody 1959), digit lengths are anatomically controlled features, and it is therefore hypothesized that these two ichnospecies represent two distinct biotaxa.

3. Specimens that clustered together under the ichnospecies *L.* (*B.*) *salamandroides* could be further split into a number of separate groups, according to size. However, analysis of manus footlength (Text-fig. 2.3) indicate that these groupings have no taxonomic significance, as they demonstrate a continuous size range amongst the *L.* (*B.*) *salamandroides* specimens and not separate groupings that may reflect distinct family generations or different biotaxa. Indeed, it is suggested that *L.* (*B.*) *salamandroides*, in exhibiting this continuous size range, represents a single discrete population that comprises members of a single biotaxon. Nevertheless, a wide range of preservational styles is exhibited within this ichnospecies (Text-fig. 3.3), and this is attributed to differences in substrate consistency at the time of imprinting, or differences in trackmaker behaviour. In contrast, the range of preservational style present in *L.* (*B.*) *plainvillensis* is attributable only to variations in substrate consistency, not trackmaker size (Text-fig. 3.2).



TEXT-FIG. 2.2. Bivariate scatter plots illustrating size divergence between the ichnospecies of *Limnopus*, in terms of trackway pattern (A) and foot morphology (B). The trend of size increase indicates allometrical growth within the associated biospecies. A, scatter plot of manus trackwidth onto manus stride; B, scatter plot of manus digit III length onto manus maximum heel length.

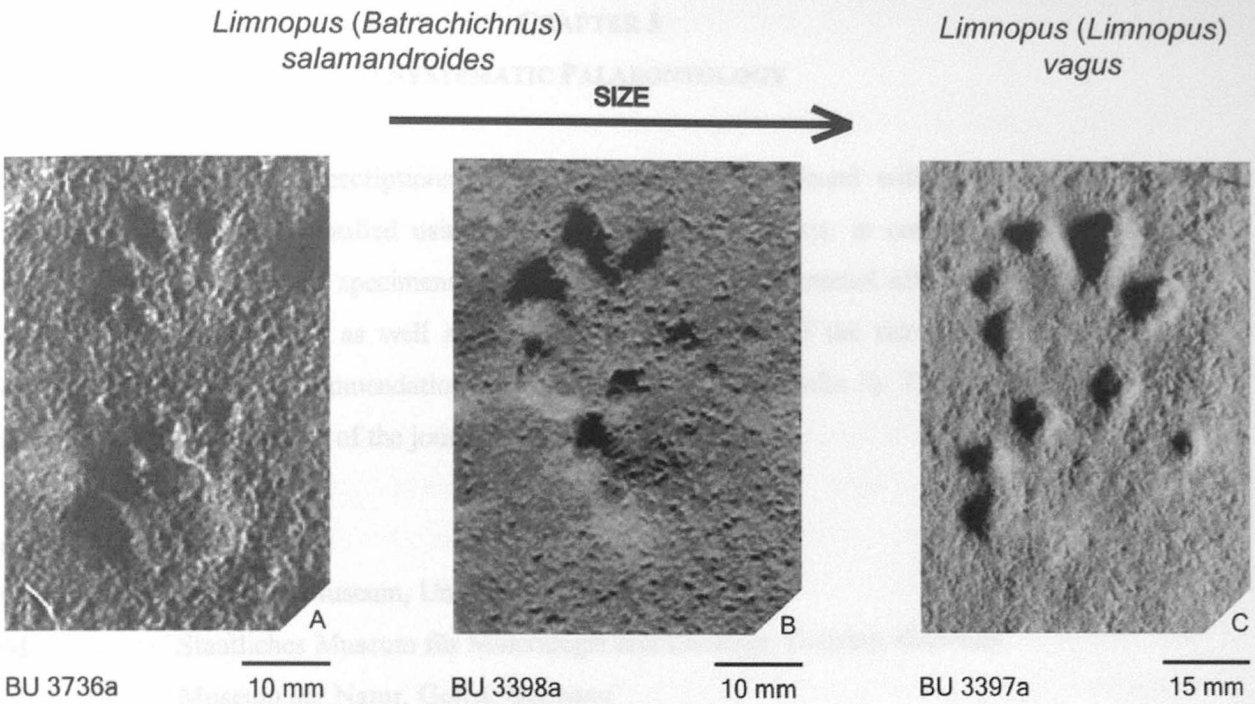


TEXT-FIG. 2.3. Plot of manus footlength within *Limnopus* (*Batrachichnus*) *salamandroides*, illustrating the continuous size range within this ichnospecies.

4. Limnopus (*Limnopus*) and *Limnopus* (*Batrachichnus*) are morphologically very similar, but show considerable size variation (Text-fig. 2.4). However, a variety of bivariate plots of morphological characters (Text-fig. 2.2A, B) indicate that the two ichnosubgenera are distinct and plot as discrete clusters on a trend of positive allometry. The plot of manus digit III length against manus maximum heel length (Text-fig. 2.2B) also shows two statistical populations within the *Limnopus* (*Limnopus*) region, but this is based on a small number of specimens and is not reflected in other bivariate plots (Text-fig. 2.2A). In the absence of further material, it is not possible to develop firm conclusions about this latter distribution and a conservative taxonomic approach is adopted here, with all specimens assigned to *Limnopus* (*Limnopus*) *vagus*.

5. *Limnopus* (*Limnopus*) *vagus* is represented by trackways exhibiting two dominant preservational styles, related to the size of the trackmaker (Text-fig. 3.1B, D). However, these can be demonstrated to pertain to the same type of trackmaker by specimens showing a transitional preservational stage.

6. It is clear that *Limnopus* (*Limnopus*) *vagus* could represent the traces of an adult version of the *Limnopus* (*Batrachichnus*) trackmaker. However, it is also highly possible that *Limnopus* (*Limnopus*) and *Limnopus* (*Batrachichnus*) could be the representatives of two different biotaxa of two discrete size ranges. Retaining separate binomina emphasises this possibility, enables a more detailed taxonomic description of specimens, and helps to stabilise ichnotaxonomy by maintaining frequently used, well-established names.



TEXT-FIG. 2.4. *Limnopus* Marsh 1894; Alveley Member, Salop Formation, Warwickshire Group. Westphalian D, Shropshire, UK. Selected manus-pes sets illustrating morphological similarity between *Limnopus* (*Batrachichnus*) and *Limnopus* (*Limnopus*). A, *L.* (*Batrachichnus*) *salamandroides*, BU 3736. B, *L.* (*Batrachichnus*) *salamandroides*, BU 3398a. C, *L.* (*Limnopus*) *vagus*, BU 3397a.

CHAPTER 3

SYSTEMATIC PALAEONTOLOGY

The following systematic descriptions refer to those ichnotaxa found within the Alveley ichno-assemblage. These were identified using multivariate cluster analysis, in conjunction with constant referral back to the original specimens. Synonymy lists were constructed after study of material in Europe and North America, as well as a comprehensive review of the relevant literature, and are annotated following the recommendations of Matthews (1973; Appendix 3). This chapter is formatted according to the requirements of the journal *Palaeontology*.

Institutional abbreviations

BU	Lapworth Museum, University of Birmingham, UK
DM	Staatliches Museum für Mineralogie und Geologie, Dresden, Germany
GN	Museum der Natur, Gotha, Germany
MCZ	Museum of Comparative Zoology, Harvard University, Massachusetts, USA
USNM	United States National Museum, Smithsonian Institution, Washington, USA
WVU	West Virginia University, USA
YPM	Yale Peabody Museum, Yale University, New Haven, USA

All material described below, unless stated otherwise, is from Butts Quarry, Alveley, Shropshire, UK, from the Alveley Member of the Salop Formation (Warwickshire Group), and is housed at the Lapworth Museum, University of Birmingham, UK.

Ichnogenus LIMNOPUS Marsh, 1894

Type ichnospecies. By monotypy; *Limnopus vagus* Marsh, 1894. Late Pennsylvanian (Kasimovian–Gzelian), Virgil Series, Howard Limestone, Osage County, Kansas, USA. Type specimen YPM 532.

Included ichnosubgenera. Limnopus (*Limnopus*) Marsh, 1894; *Limnopus* (*Batrachichnus*) Woodworth, 1900.

Diagnosis (emended after Haubold 1971*a*). Quadrupedal trackway with pes pace angulation of 74–96°. Pes impression commonly placed closely behind the manus impression. Stride:footlength ratio varies from 3·1 to 7·6. Tetradactyl manus, with short, broad digits; lengths progress from I-II-III, IV equal to II. Digit III is directed parallel to or curves towards the trackway midline. Pentadactyl pes, up to 135 mm long, with digit V frequently missing. Digit lengths increase I-II-III-IV, V equal to II. Sole pad is proximally broadly rounded in well-preserved tracks, although extra-morphological influences may produce a U-shaped heel. The basal pads of digit I of both the manus and the pes are usually impressed. Manus and pes digits with rounded tips.

Remarks. The ichnogenus *Limnopus* was erected by Marsh (1894), in conjunction with the ichnotaxa *Baropus lentus* and *Allopus littoralis*. These three ichnogenera were synonymized and refigured by Baird (1952), who chose *Limnopus* as the available name and synonymized the ichnospecies *Allopus littoralis* and *Baropus lentus*, with the original specimen of *A. littoralis* (YPM 207) as the type. Haubold (1971*b*) subsequently synonymized *L. littoralis* with *L. waynesburgensis* (Tilton 1931), which had first been assigned by Tilton (1931) to the ichnogenus *Baropus*. In addition, Haubold (1971*a*) noted the similarity between *Limnopus* and *Nanopus*, although he did not synonymize the two. *Limnopus zeilleri* (Delage 1912) is not considered to belong to the ichnogenus *Limnopus*, as reference to the original figured specimens, which are unclear (Delage 1912; Haubold 1971*a*), suggests that *L. zeilleri* is very distinct from the type ichnospecies, *L. vagus*. *Limnopus* is a stable ichnogenus, which may represent the large (possibly adult) form of *Batrachichnus*. Haubold (1971*a*) first recognized the similarity between these two ichnogenera, noting that the digit arrangements closely correlate with the anatomy of the Eryopoidea (stem-lissamphibia of Ruta and Coates in press). Haubold (*pers. comm.* 2002) argues that it is possible for *Limnopus* and *Batrachichnus* to represent trackmakers of different biotaxa and therefore that separate ichnotaxa should be retained. In agreement with this statement, and in order to retain taxonomic stability whilst recognizing the obvious similarities between *Limnopus* and *Batrachichnus*, *Limnopus* is here divided into two ichnosubgenera, *Limnopus* (*Limnopus*) and *Limnopus* (*Batrachichnus*). This is based upon the numerical, multivariate analysis of a large number of *Batrachichnus* and *Limnopus* specimens, as outlined above. Whilst in terms of foot size *Limnopus* splits into three groups (Text-fig. 2.2B), the intermediate size group is

included under *Limnopus* (*Limnopus*) *vagus*, as these specimens fit within the diagnosis of this ichnospecies. Bivariate plots based upon trackway pattern (Text-fig. 2.2A) clearly illustrate the distinction between *Limnopus* (*Limnopus*) and *Limnopus* (*Batrachichnus*). Principal Component Analysis confirms that the principal component of dissimilarity (96 per cent) between these two ichnosubgenera is one of size (Text-fig. 2.4), which varies within a continuous range across the measured specimens. The second component (3·9 per cent) is based upon digit and print angulations, which were shown by Peabody (1959) to vary widely within biospecies as a result of trackmaker speed and substrate consistency. Other components have negligible significance. Therefore, as size is not considered an ichnogenerically diagnostic character, and digit/print angulations are variable dependent upon environmental factors, *Limnopus* Marsh, 1894 and *Batrachichnus* Woodworth, 1900 are here classified as ichnosubgenera of the senior name. In addition, *Batrachichnus* is synonymous with *Anthichnium* Nopsca, 1923. Haubold (1971*a*) assigned *Limnopus* to either the Edopsoidea or the Eryopoidea, based upon the fact that there are few other large terrestrial amphibians of that age with tetradactyl manus morphology and ossified tarsals, suggested by the distinct sole impression of *Limnopus*. Both of these families were interpreted as stem-lissamphibian clades in the analysis of Ruta *et al.* (2003). The lack of abundant skeletal remains of large, terrestrial, Upper Palaeozoic amphibians renders generic identification of the trackmaker difficult; nevertheless, recent work has led Haubold (2000) to suggest the genus *Eryops* as the most likely trackmaker of *Limnopus*. The appearance of *Limnopus* in the Alveley ichno-assemblage extends the stratigraphical range of this ichnogenus from the mid-Kungurian (Lower Rotliegendes, mid-Permian) back to the late Moscovian (lower Pennsylvanian, Late Carboniferous).

Stratigraphical range. Late Moscovian to mid-Kungurian.

Ichnosubgenus LIMNOPUS (LIMNOPUS) Marsh, 1894

Included ichnospecies. Limnopus cutlerensis Baird, 1965, from the Early Permian Cutler Formation of San Miguel County, Colorado, USA; *L. haussei* (Schmidt, 1959), from the Early Permian (Lower Rotliegend) of the Döhlen Basin, Dresden, Sachsen; *L. regularis* (Heyler and Lessertisseur, 1963) from the Early Permian of Lodève, Herault, France.

Type ichnospecies. As for ichnogenus.

Limnopus (*Limnopus*) *vagus* Marsh, 1894

Text-figures 2.4C, 3.1A–D

* v	1894	*Limnopus vagus* Marsh, p. 82, pl. 2, fig. 2, pl. 3, fig. 2.
v	1894	*Baropus lentus* Marsh, p. 83, pl. 2, fig. 5.
v	1894	*Allopus littoralis* Marsh, p. 83, pl. 2, figs 4–4a.
v	1926	'stegocephalian or reptile' Tilton, p. 389–391, pl. 11, figs A–E.
v	1927	*Baropus lentus* Marsh; Gilmore, p. 23, text-fig. 10.
v	1927	*Baropus coconinoensis* Gilmore, pp. 24–26, text-fig. 9, pl. 7.
v	1931	*Baropus waynesburgensis* Tilton, pp. 551–555, text-fig. 4, table 2.
	1952	*Limnopus vagus* Marsh; Baird, pp. 834–836, pl. 122, text-figs 1–2, table 1.
	1952	*Limnopus littoralis* (Marsh); Baird, pp. 836–837, pl. 123–124, figs 1–3, text-fig. 3.
v	1952	*Limnopus waynesburgensis* (Tilton); Baird, pp. 837–838, pl. 124, fig. 4, text-fig. 4.
	1965	*Limnopus cutlerensis* Baird, p. 47, text-figs 14B–C.
	1970	*Limnopus vagus* Marsh; Haubold, p. 96, text-fig. 5B [*kop.* Baird 1952, text-fig. 2].
	1970	*Limnopus cutlerensis* Baird; Haubold, p. 96, text-fig. 5D.
	1970	*Limnopus littoralis* (Marsh); Haubold, p. 96, text-fig. 5H [*kop.* Baird 1952, text-fig. 3].
	1970	*Limnopus waynesburgensis* (Tilton); Haubold, p. 96, text-fig. 5G [*kop.* Baird 1952, text-fig. 4].
v	1971*a*	*Limnopus vagus* Marsh; Haubold, p. 17, text-fig. 12.5.
?	1971*a*	*Amphisauroides minor* (Heyler and Lessertisseur); Haubold, p. 21, text-fig. 14.3.
v	1973	*Limnopus rawi* Haubold and Sarjeant, pp. 899–900, pl. 3, text-fig. 2.4.
v	1974	*Limnopus rawi* Haubold and Sarjeant; Haubold and Sarjeant, p. 260, text-

		fig. 2.
	1987	*Limnopus zeilleri* (Delage); Gand, p. 98, pl. 2E (non pl. 2A–D, 2F), text-figs 28–30, tables 43–50.
v	1990	*Limnopus vagus* Marsh; *Hunt et al.*, p. 292, text-figs 3B, 4F.
p	1995	*Limnopus vagus* Marsh; Hunt *et al.*, p. 264, text-fig. 2F (non text-fig. 2E).
v	1995	*Limnopus* sp.; Haubold *et al.*, pp. 143–145, text-fig. 7B–C.

Material. BU 2471b; 3397a; 3400a; 3402–3403; 3405c; 3410c; 3689a; 3706b; 3707a; 3714a.

Diagnosis (emended from Baird 1952). Species of *Limnopus* (*Limnopus*) with pes slightly longer than wide, print angulation 39–100°, pes print angulation 70–123°. Pes impressed posterior and somewhat lateral to manus, occasionally overlapping it slightly. Manus footlength 26–40 mm, pes footlength 29–48 mm.

Description

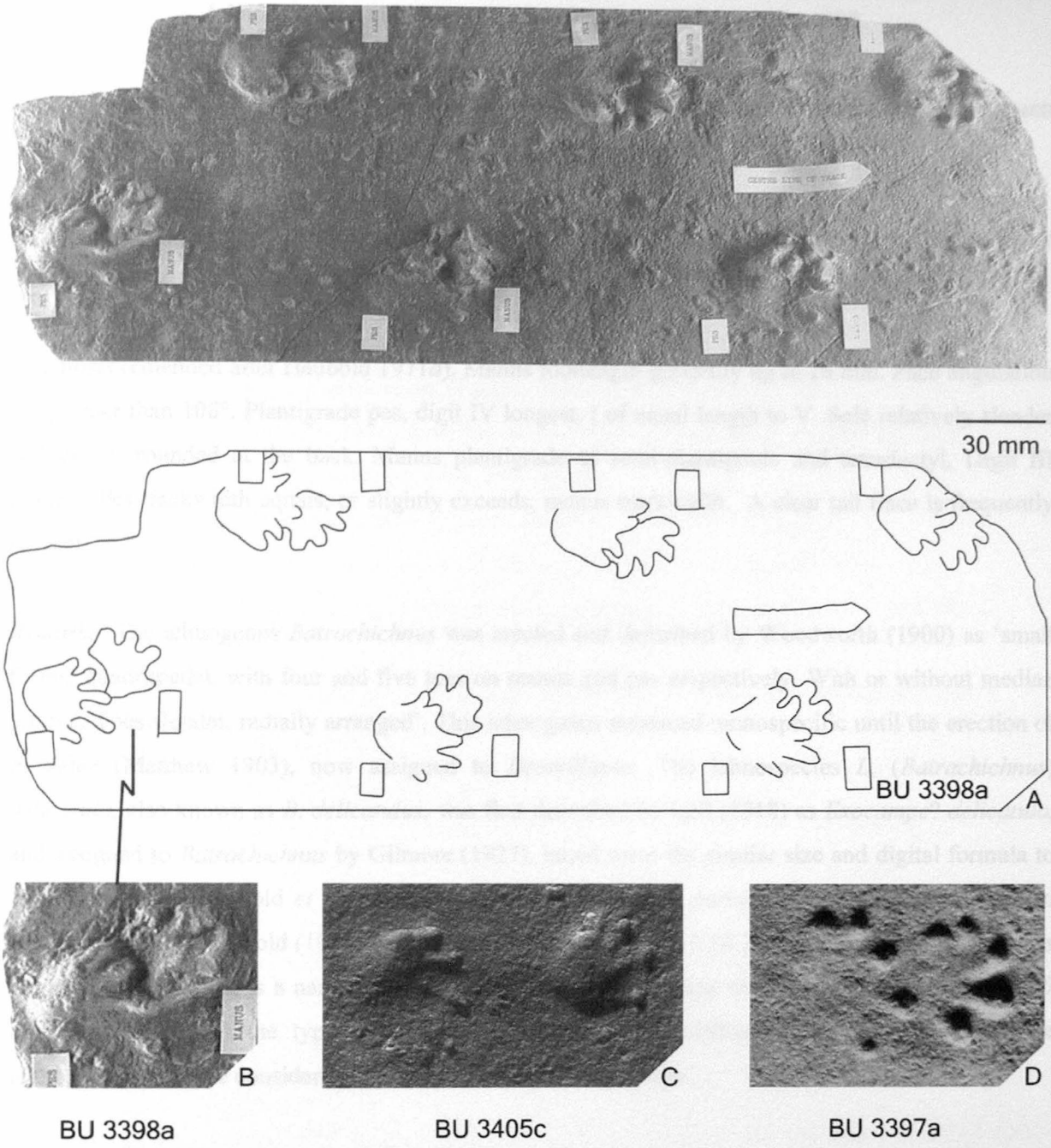
Manus morphology. Tetradactyl, fully plantigrade to semi-digitigrade. Footwidth (25–41 mm) greater than footlength (21–40 mm). All four digits distinct; impression strength increases distally along digits, and in some specimens (BU 3397a, 3689a) decreases medially. Digits short, broad and distally tapering, with rounded tips and medial curvature. Digit III, the longest digit, 8–18 mm from hypex, is the most curved; digits I and IV almost straight. Total digit angulation 65–95°. Sole appears uniformly padded, but digits of overlapping pes obscure heel imprint, which is relatively short (10–27 mm), broad (8–28 mm) and convex, or with square base.

Pes morphology. Pentadactyl, plantigrade to digitigrade, although digits IV–V may not always be preserved. Footlength (29–48 mm) greater than footwidth (18–47 mm). Impression strength increases distally along digits. Digits relatively long and slender, and taper distally to a rounded tip. Digits I to IV strongly impressed, with medial increase in impression strength. Digit V represented by faint digit tip outline only, giving total digit angulation of 70–86°, whilst angulation between digits I–IV varies from 48–79°. Digit I is most strongly impressed, with oval, broad sole pad at base. Digit IV is longest, 12–25 mm long from hypex. Digits I, II and V straight, whilst digits III and IV curve slightly laterally. Sole uniformly padded, with extended, elongate heel (10–32 mm long) that tapers distally (heel width 3 mm from posterior termination equals 10–20 mm).

Trackway Structure. Manus–pes overlap variable (from 14 mm overlap of manus by pes, to 16 mm distance between manus heel and pes digit tip III). Manus prints turned slightly medially (manus print angulation 39–100°), whilst pes prints range from medially facing to slightly laterally facing (pes print

angulation 70–123°). Pes trackwidth narrow in comparison to pes footwidth (pes trackwidth 84–114 mm), but greater than manus trackwidth (50–101 mm). Manus pace angulations 74–109° and pes pace angulations 65–95°. Manus stride:footlength 3·9–7·6, pes stride:footlength 3·4–5·7. Manus stride 112–179 mm, manus pace 83–123 mm; pes stride 132–182 mm, pes pace 116–152 mm.

Remarks. Haubold and Sarjeant (1973, 1974) erected a new ichnospecies, *Limnopus rawi*, to describe the specimens of *Limnopus* (*Limnopus*) within the Alveley ichno-assemblage. However, this ichnospecies was erected purely to refer to specimens of *Limnopus* (*Limnopus*) from Shropshire, UK, and was not based upon significant morphological traits. Consequently, *Limnopus rawi* is here considered to be a junior synonym of *L.* (*L.*) *vagus*. The ichnospecies is represented within the Alveley ichno-assemblage predominantly by two styles of preservation (Text-figs 3.1B, D), related to trackmaker size, with one specimen (BU 3405c, Text-fig. 3.1C) exhibiting a transitional stage. This enables the two preservational styles to be attributed to the same type of trackmaker and therefore the same ichnospecies. Larger specimens (Text-fig. 3.1B) are more deeply impressed than smaller trackways, and therefore preserve the entire length of the digits, whilst in smaller specimens these may appear as tip marks only (Text-fig. 3.1D). This shallower style of preservation is similar to that of the type specimen of *L.* (*L.*) *vagus*. Comparison of *L.* (*L.*) trackways with those of *L.* (*B.*) demonstrates that the most significant difference between these ichnotaxa is one of size (Text-fig. 2.4). In terms of foot morphology, *L.* (*L.*) *vagus* can be split into three statistical populations according to size difference (Text-fig. 2.2B), but in terms of trackway pattern (Text-fig. 2.2A), *L.* (*L.*) *vagus* separates clearly from *Limnopus* (*Batrachichnus*).



TEXT-FIG. 3.1. *Limnopus* (*Limnopus*) *vagus* Marsh, 1894; Alveley Member, Salop Formation, Warwickshire Group. Westphalian D, Shropshire, UK. A, BU 3403a, type specimen of *Limnopus rawi* Haubold and Sarjeant, 1973, with interpretative drawing. B–D, selected manus-pes sets illustrating preservational variation within the ichnospecies. B, BU 3398a, manus footlength is 24 mm. C, BU 3405c, manus footlength is 22 mm. D, BU 3397a, manus footlength is 20 mm.

Ichnosubgenus LIMNOPUS (BATRACHICHNUS) Woodworth, 1900

Type ichnospecies. Batrachichnus plainvillensis Woodworth, 1900. Late Carboniferous, Narragansett Basin, Plainville, Wrentham, Massachusetts, USA. Type specimen MCZ 1052.

Included ichnospecies. Limnopus (*Batrachichnus*) *salamandroides*, from the Early Permian of Thüringer Wald, Germany.

Diagnosis (emended after Haubold 1971*a*). Manus footlength generally up to 26 mm. Pace angulation not greater than 108°. Plantigrade pes, digit IV longest, I of equal length to V. Sole relatively slender and gently rounded at the back. Manus plantigrade to semi-plantigrade and tetradactyl, Digit III longest. Pes trackwidth equals, or slightly exceeds, manus trackwidth. A clear tail trace is frequently present.

Remarks. The ichnogenus *Batrachichnus* was erected and described by Woodworth (1900) as 'small forms, quadrupedal, with four and five toes on manus and pes respectively. With or without median groove. Toes slender, radially arranged'. This ichnogenus remained monospecific until the erection of *B. celer* (Matthew 1903), now assigned to *Dromillopus*. The ichnospecies *L.* (*Batrachichnus*) *delicatula*, also known as *B. delicatulus*, was first described by Lull (1918) as *Exocampe*? *delicatula*, and assigned to *Batrachichnus* by Gilmore (1927), based upon the similar size and digital formula to *B. plainvillensis*. Haubold *et al.* (1996) noted that *Dromillopus parvus* Gilmore, 1927, assigned to *Batrachichnus* by Haubold (1971*a*), is a preservational variant of *L* (*B.*) *delicatulus*, as is *B. obscurus* Gilmore, 1927, which is a name pertaining to very small trackways with a pes length of less than 5 mm. After study of the type specimens of *D. parvus*, *E?. delicatula* and *B. obscurus*, these ichnospecies are here considered to belong to *L.* (*B.*) *plainvillensis*.

Stratigraphical range. Late Moscovian to mid-Kungurian.

Limnopus (Batrachichnus) plainvillensis Woodworth, 1900

Text-figures 3.2A–F

?	1891	*Notalacerta jacksonensis* Butts, p. 18, text-fig. 2.
v	1918	*Exocampe*? *delicatula* Lull, pp. 344–346, text-fig. 4, pl. 3, fig. I.
* v	1900	*Batrachichnus plainvillensis* Woodworth, pp. 452–453, pl. 40, fig. 1, text-fig. 2.
v	1912	*Ichnium dolichodactylum* Pabst; Hardaker, pp. 669–670, text-fig. 22.
v	1927	*Batrachichnus delicatula* (Lull); Gilmore, pp. 36–40, text-figs 15, 16 [*kop.*

		Lull 1918, text-fig 4], pl. 12.
	1927	*Batrachichnus obscurus* Gilmore, pp. 40–42, text-figs 17, 18 [kop. Woodworth 1900], pl. 12.
v	1927	*Dromillopus parvus* Gilmore, pp. 42–45, text-figs 19–20, pl. 14.
v	*1970*	*Batrachichnus plainvillensis* Woodworth; Haubold, p. 92, text-fig. 3A [*kop.* Woodworth 1900, text-fig. 2].
v	1970	?*Batrachichnus parvus* (Gilmore); Haubold, p. 92, text-fig. 3B [*kop.* Gilmore 1927, text-fig. 19].
	1970	*Amphisauroides* sp. (Pabst); Haubold, p. 104, text-fig. 7E.
v	1971*a*	*Batrachichnus plainvillensis* Woodworth; Haubold, p. 14, text-fig. 10.8 [*kop.* Woodworth 1900, text-fig. 2].
?	1971*a*	*Nanipes delicatus* Gilmore; Haubold, p. 14, text-fig. 10.5.
v	1971*a*	*Batrachichnus parvus* (Gilmore); Haubold, p. 14, text-fig. 10.9.
v	1973	*Batrachichnus alveleyensis* Haubold and Sarjeant, p. 899, pl. 1, text-figs 2–3.
v	1974	*Batrachichnus alveleyensis* Haubold and Sarjeant; Haubold and Sarjeant, p. 260, text-fig. 1.
	1981	*Batrachichnus hunecki* Holub and Kozur, pp. 166–167, pl. 6, figs 1, 3.
v	1995	*Batrachichnus delicatulus* (Lull); Hunt *et al.*, pp. 168–171, text-fig. 2.
	1995	*Batrachichnus plainvillensis* Woodworth; Schult, p. 117, text-fig. 5.
?	1995	*Dromillopus quadrifidus* Matthew; Schult, p. 118, text-fig. 9.
	1996	*Batrachichnus salamandroides* (Geinitz); Haubold, pp. 37–48, text-fig. 8A.

Material. BU 3398b; 3403b; 3413a; 3434b; 3693a.

Diagnosis. An ichnospecies of *Limnopus* (*Batrachichnus*) with manus and pes stride up to 74 mm. Relatively low trackwidth (manus trackwidth up to 37 mm; pes trackwidth up to 41 mm), with correspondingly low pace angulation, up to 108°.

Description

Manus morphology. Tetradactyl manus, footlength (5–15 mm) slightly greater than footwidth (7–12 mm). Deep, plantigrade impressions may render digits indistinguishable, but well-preserved specimens show relatively short, slender, distally tapering digits with rounded tips. Digit III longest (up to 13 mm), and total digit divarification is 48–102°. Digits vary from straight to slightly medially curved; this curvature decreases from digits I to IV. Stride 29–74 mm; pace 21–51 mm. Well-preserved heel is square with concave base and uniformly padded with strongly imprinted sole.

Alternatively, heel may appear more strongly impressed at bases of digits I and IV. Impression strength increases distally along digits.

Pes morphology. Pentadactyl, although digit V often not preserved along entire length. Pes is slightly larger than manus; footlength (8–19 mm) greater than footwidth (5–13 mm). Tracks deeply imprinted, yet pes digits more frequently distinctly preserved than those of manus. Digit I frequently best preserved, with elongate sole pad at base. Long, slender digits with mean total angulation of 71° (Digits I–V), whilst digits I–IV have mean angulation of 57°. Digit IV is longest (up to 20 mm). Digits may taper distally or maintain constant breadth along length; all digits vary from straight to slightly medially curved. In less well-preserved specimens, only digits I–III may be impressed. Stride 29–74 mm, pace 22–63 mm. Strongly imprinted, uniformly padded, elongate sole with rounded heel, which may appear pointed in less well-preserved specimens.

Trackway structure. There is no evidence for the characteristic *Limnopus* (*Batrachichnus*) tail trace in any of the surface trackway specimens from the Alveley ichno-assemblage. Both manus and pes prints frequently face forward in alignment with trackway midline, although manus occasionally has slight inward (medial) turn towards trackway midline. Overlapping of manus by pes is rare, occurring in only 6 per cent of manus–pes sets, although manus–pes distance is variable (distance between manus heel and pes digit tips from 0–10 mm). Pes trackwidth (20–41 mm) greater than manus trackwidth (12–37 mm), fitting with original description of *Batrachichnus plainvillensis* and contrary to first description of *B. alveleyensis* (Haubold and Sarjeant 1973). Pace angulation characteristically low (61° to 108°). Regular manus–pes set pattern.

Undertracks. Material: BU 3397b; 3400c, d; 3408a; 3430a; 3690a; 3692b; 3695a; 3708b; 3709b; 3711a; 3712b, c; 3715b, d; 3716c, d; 3719a; 3726a, b; 3728a; 3730c, d; 3731d; 3733c; 3735a; 3736a; 3738c; 3739b; 3742a; 3743a; 3744a; 3745a; 3746a; 3748b; 3750b. *Limnopus* (*Batrachichnus*) is also preserved as numerous undertracks, represented by deep impressions peaking at footprint centre with indistinguishable digits. Manus–pes sets regularly placed, although distance between manus and pes is variable, accordant with above description. Pes larger than manus (mean size of pes tracks 6–10 mm, manus tracks 4–5 mm), and preserves longer, more elongate heel impression. Prints appear to face forward with respect to trackway midline. Pes trackwidth may be slightly greater than, or equal to manus trackwidth. Deeper undertracks appear as elongate ovals where manus and pes impressions have merged.

Remarks. Notalacerta jacksonensis Butts, 1891, is here tentatively assigned to *L.* (*B.*) *plainvillensis*, based upon the original description and figured specimen (Butts 1891). *N. jacksonensis* has previously been considered by various authors (e.g. Gilmore 1927; Haubold 1971*a*) to bear no resemblance to the

type specimen of *Notalacerta, N. missouriensis* Butts, 1891. However, the original specimen of *N. jacksonensis* is not figured well enough to render the present assignation to *L.* (*B.*) *plainvillensis* certain. *Batrachichnus alveleyensis* Haubold and Sarjeant 1973 (BU 3398, Text-figs 3.2D–E), is assigned to *L.* (*B.*) *plainvillensis*, as the original diagnosis of *B. alveleyensis* rests upon the lack of tail trace in the type specimen. However, Gilmore (1927) noted (after Matthew 1903) that *B. plainvillensis* may also lack a 'median groove'. Therefore, *B. alveleyensis* is here assigned to *L.* (*B.*) *plainvillensis*, as the absence of a tail trace in *B. alveleyensis* is the only significant difference between the two specimens, and this absence may be simply due to substrate conditions (Peabody 1959). Indeed, the preservational style of *L.* (*B.*) *plainvillensis* within the Alveley ichno-assemblage is highly variable due to differences in substrate conditions (Text-fig. 3.2B–F). This re-assignation of *B. alveleyensis* is additionally supported by results of the multivariate statistical analysis carried out on a number of trackways from the Alveley ichno-assemblage, including numerical data on the holotype specimen (MCZ 1052) of *B. plainvillensis*, as given by Woodworth (1900) and Haubold (1973). *Dromillopus* Matthew, 1904, as represented by the type ichnospecies, *Dromillopus quadrifidus*, is recognized as an ichnogenus similar to, yet distinct at an ichnogeneric level, from *Limnopus* (*Batrachichnus*). This similarity led some leading subsequent authors to attribute specimens of *B. plainvillensis* to *D. quadrifidus* (e.g. Schult 1996). However, the ichnotaxonomic assignations of Schult (1996) cannot be checked with certainty as specimen numbers were not supplied. In his description of *Batrachichnus*, Woodworth (1900) proposed that 'stegocephalians' might be the responsible biotaxa, and suggested *Amphibamus* (Carboniferous, Ohio), or an unknown form with a tetradactyl manus, of similar size and shape to *Melanerpeton* from the Permian of Germany, as possible trackmakers. Haubold (1971*a*) assigned *Batrachichnus* to the Superfamily Edopoidea (stem-lissamphibia, or 'temnospondyls'), due to the similar tetradactyl manus morphology. He suggested *Dendrerpeton* as a possible trackmaker,' however this generic designation was based only upon a lack of morphological features providing evidence to the contrary. More recent work has led Haubold (2000) to attribute *Batrachichnus*, as a possible juvenile form of *Limnopus*, to *Eryops*.

Limnopus (Batrachichnus) salamandroides (Geinitz, 1861)

Text-figures 2.4A–B, 3.3A–D

* 1861 *Saurichnites salamandroides* Geinitz, p. 4, pl. 1.

1897 *Ichnium tetradactylum* Pabst, p. 87, text-figs 3–4.

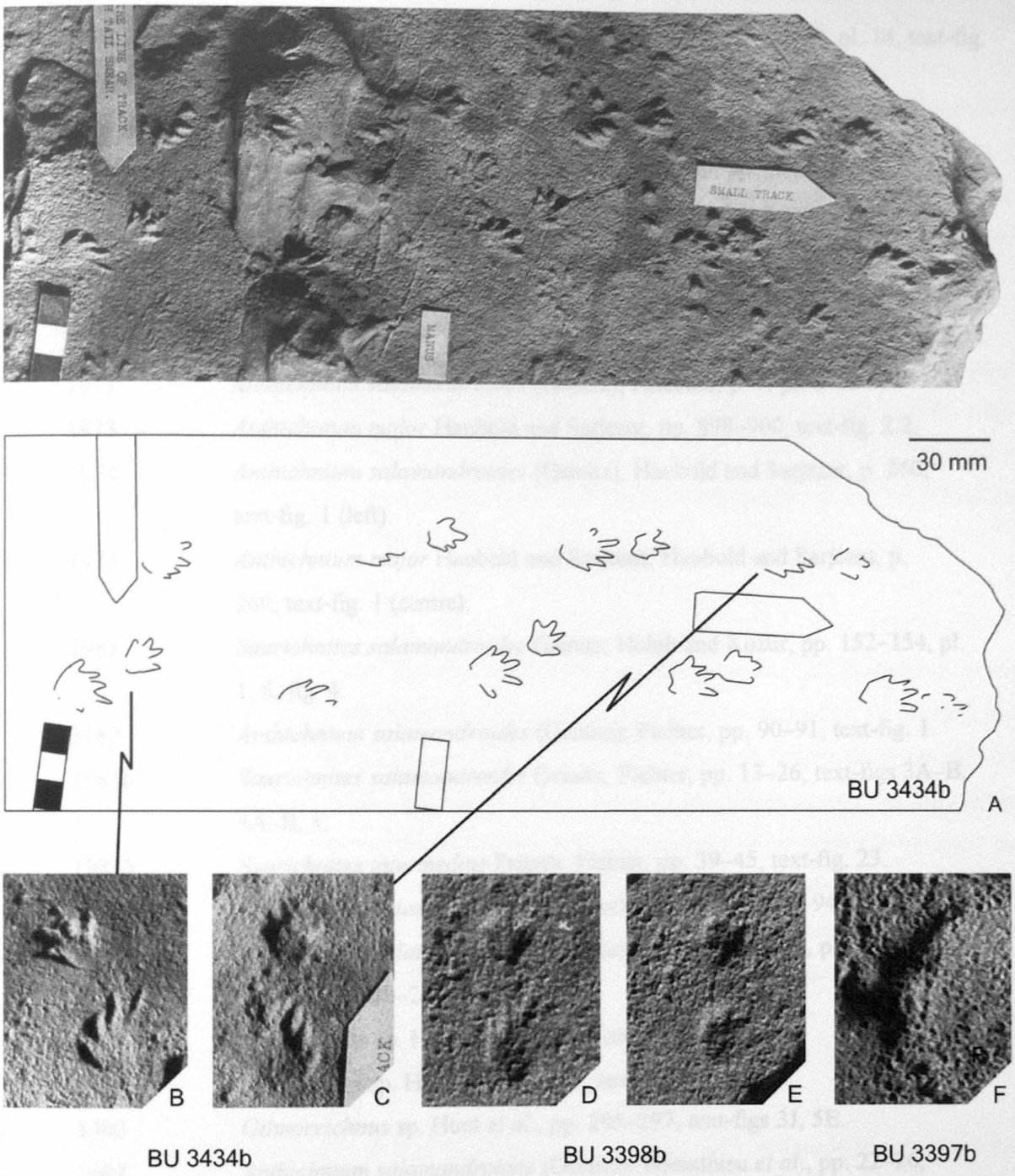
1900 *Ichnium anakolodactylum* Pabst, pp. 55, 60.

1905 *Ichnium rhopalodactylum* Pabst, p. 10.

1905 *Ichnium kalnanum* Pabst, p. 10.

1908 *Ichnium anakolodactylum* Pabst; Pabst, p. 93, pl. 23, figs 2–3, text-fig. 31.

1923 *Anthichnium anacolydactylum* Nopsca, p. 135.



TEXT-FIG. 3.2. *Limnopus* (*Batrachichnus*) *plainvillensis* Woodworth 1900; Alveley Member, Salop Formation, Warwickshire Group. Westphalian D, Shropshire, UK. A, BU 3434b with interpretative drawing. B–F, selected manus-pes sets illustrating preservational variation within the ichnospecies. Scale: manus footlength is 8 mm. B–C, BU 3434b. D–E, BU 3398b, type specimen of *Batrachichnus alveleyensis* Haubold and Sarjeant, 1973. F, BU 3397b.

	1970	*Anthichnium salamandroides* (Geinitz); Haubold, pp. 89–92, pl. 14, text-fig. 3E.
	1970	*Amphisauropus imminutus*; Haubold, pp. 103–104, pl. 20, text-fig. 7D.
	1971*b*	*Anthichnium salamandroides* (Geinitz); Haubold, pp. 19–20, pl. 5, fig. 1.
	1972	*Anthichnium salamandroides* (Geinitz); Haubold and Katzung, pp. 889–895, text-fig. 2.1.
v	1973	*Anthichnium salamandroides* (Geinitz); Haubold and Sarjeant, pp. 897–899, text-fig. 2.1.
	1973	*Anthichnium salamandroides* (Geinitz); Haubold, p. 7, pl. 6–7.
v	1973	*Anthichnium major* Haubold and Sarjeant, pp. 898–900, text-fig. 2.2.
v	1974	*Anthichnium salamandroides* (Geinitz); Haubold and Sarjeant, p. 260, text-fig. 1 (left).
v	1974	*Anthichnium major* Haubold and Sarjeant; Haubold and Sarjeant, p. 260, text-fig. 1 (centre).
	1981	*Saurichnites salamandroides* Geinitz; Holub and Kozur, pp. 152–154, pl. 1, 6, fig. 4.
	1982	*Anthichnium salamandroides* (Geinitz); Fichter, pp. 90–91, text-fig. 1.
	1983*b*	*Saurichnites salamandroides* Geinitz; Fichter, pp. 13–26, text-figs 3A–B, 4A–B, 5.
?	1983*b*	*Saurichnites intermedius* Fritsch; Fichter, pp. 39–45, text-fig. 23.
	1985	*Anthichnium salamandroides* (Geinitz); Haubold, pp. 93–94.
p	1987	*Anthichnium salamandroides* (Geinitz); Gand, pp. 75–98, pl. 3A–D, 3F (*non* 3E) text-figs 20–23, tables 25–42.
v	1990	*Anthichnium* sp. Hunt *et al.*, p. 292, text-fig. 3A.
v	1990	cf. *Nanopus* sp. Hunt *et al.*, p. 295, text-figs 3C, 4E.
v	1990	*Gilmoreichnus* sp. Hunt *et al.*, pp. 295–297, text-figs 3J, 5E.
?	1992	*Anthichnium salamandroides* (Geinitz); Demathieu *et al.*, pp. 22–26, text-fig. 4E.
	1995	*Anthichnium salamandroides* (Geinitz); Gand *et al.*, pp. 103–107, pl. 2, text-fig. 6B–C.
v	1996	*Batrachichnus delicatula* (Lull); Haubold *et al.*, pp.137–143, text-fig. 2A, C.
v	1996	*Batrachichnus delicatula* (Lull); Hunt *et al.*, pp. 168–171, text-fig 2A [*kop.* Haubold *et al.* 1996, text-fig 2C], C.
v	1996	*Limnopus* sp. Haubold *et al.*, pp. 143–145, text-fig. 7A.
	1996	*Batrachichnus salamandroides* (Geinitz); Haubold, pp. 37–48, text-figs. 6A–B, 8B, 10A.

Material. BU 3407a; 3408c; 3412d; 3429a; 3688a; 3694a; 3696a; 3697a, c; 3698b; 3699a; 3700b; 3701a, b; 3704a; 3705a, b; 3710d; 3711a; 3712b, c; 3713b; 3715a, e; 3716c; 3718b; 3720b, c; 3723c, d; 3724a; 3725b; 3729b, c; 3730e; 3731b, c; 3732b, d; 3735c; 3736b; 3737b; 3738b; 3740a; 3741a; 3745b, c. Incomplete and not identified in cluster analysis: 2471c, f; 3398c; 3413c; 3430a; 3432a; 3689b, c; 3690a; 3692a, b, d; 3698a; 3708b, d; 3715b, d; 3716c, d; 3719a; 3721c; 3722c; 3723a, b; 3726a; 3727a; 3728a; 3729a; 3730c, d; 3731d; 3733c; 3735a; 3736a; 3738c; 3739b; 3742a; 3743a; 3744a; 3745a; 3746a; 3747b–d; 3748b, c; 3749a; 3750b.

Diagnosis. An ichnospecies of *L.* (*Batrachichnus*) with a large stride (manus stride up to 158 mm, pes stride up to 159 mm) and trackwidth (manus trackwidth up to 68 mm, pes trackwidth up to 94 mm) in relation to footlength (between 5 and 32 mm; manus length generally up to 26 mm). Pace angulation is correspondingly high (manus pace angulation up to 128°, pes pace angulation up to 110°). Digits are slightly longer in proportion to heel length.

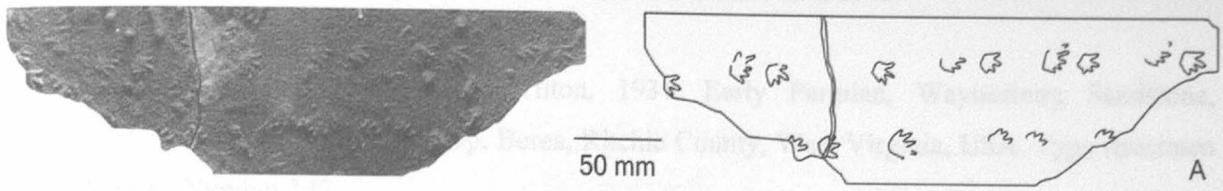
Description

Manus morphology. Tetradactyl, plantigrade manus, impressed along length, with impression strength slightly increasing distally towards digit tips. Footlength approximates footwidth (footlength 5–26 mm, footwidth 4–28 mm). Digits long (digit III longest, 2–14 mm from hypex to digit tip, length approximates 50 per cent footlength), and slender, with rounded tips. Digits straight, or very slightly medially curving. Heel square, slightly wider than long (width 2–18 mm, length 2–11 mm) with concave base. On less well-preserved specimens, imprinted only where sole extends back from base of digit I, sole appears to form rounded, bulbous pad at back of heel, altering preserved shape of the distal heel. Otherwise, sole is uniformly padded. Total digit angulation measures 50–121°. Print angulation 40–116° (i.e. manus may face inwards or outwards towards trackway midline, and can lie with long axis parallel to trackway midline).

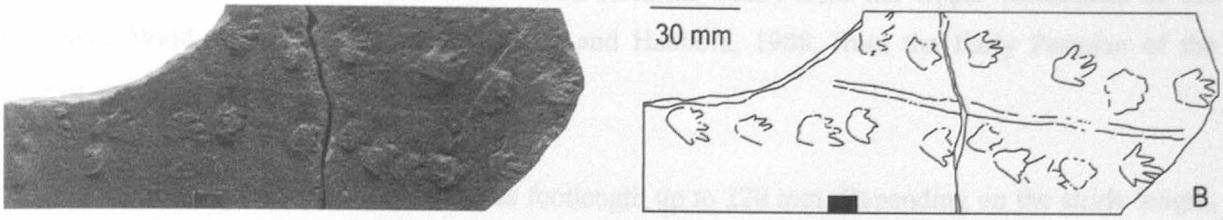
Pes morphology. Pentadactyl pes; impression strength varies from sub-digitigrade to sub-plantigrade so that in less well-preserved specimens, digits IV and V are absent, or only tips are preserved (digitigrade preservation). Digit I impressed along entire length, including where sole extends from base of digit, but remainder of sole is unimpressed. Digits long (Digit IV longest, 4–19 mm from hypex to digit tip) and slender, with constant breadth and rounded tips. Curvature ranges from very slightly medial to straight; curvature decreases from digit I to V. Heel often faint or completely unimpressed; on well-preserved trackways appears rounded and slightly tapering, with a uniformly padded sole. Heel equidimensional, with length 3–12 mm, and width 2–17 mm. Footlength 6–32 mm, footwidth 4–32 mm. Total digit angulation 32–81°; digit angulation between digits I–IV 64–89°.

Trackway structure. Distance between manus heel and pes digit III tip within a single set up to 19 mm; overlap of manus by pes is up to 8 mm. Both manus and pes prints are variable in inclination (medially or laterally facing, or in alignment with trackway midline), although inclination is predominantly medial; manus values 43–106°, pes values 65–112°. Pace angulations 51–128° for manus and 39–110° for pes. Accordingly, pes trackwidth (14–94 mm) is greater than manus trackwidth (12–68 mm). Manus stride 31–158 mm, manus pace 20–109 mm, with stride:footlength 2·9 to 9·2. Pes stride 27–159 mm, pes pace 23–128 mm; stride:footlength 2·4 to 7·0.

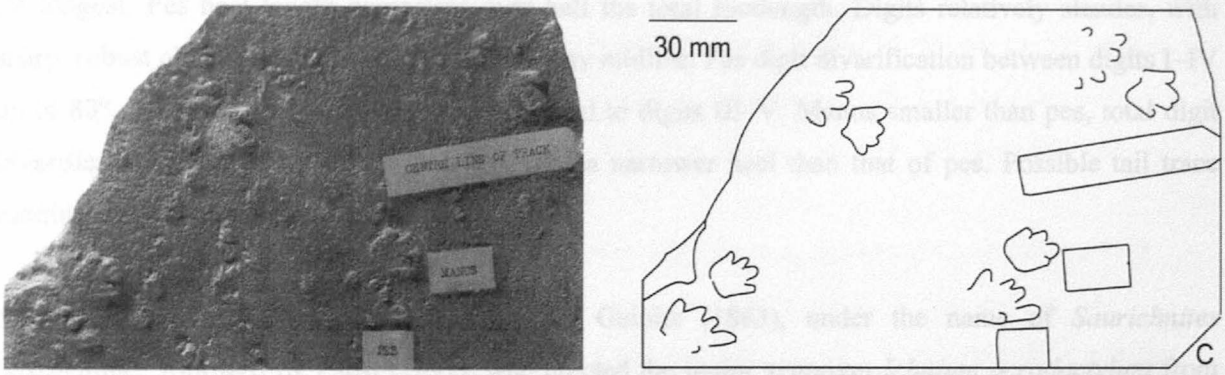
Remarks. Limnopus (*Batrachichnus*) *salamandroides* was formerly classified under the ichnogenus *Anthichnium*, erected by Nopsca (1923) with the description of the ichnospecies *Anthichnium anacolodactylum*. However, the type specimen of *Anthichnium* was described by Geinitz (1861) under the name *Saurichnites salamandroides*, assigned to *Anthichnium* by Haubold (1970). A number of forms were described under the ichnogenus *Ichnium* by Pabst (1897, 1900, 1905, 1908), the species names of which were supposed to illustrate the preservational form of the digits. These forms have since been recognized as morphological variants of the *Anthichnium* type ichnospecies, *A. salamandroides*. Haubold (1971*a*) recognized the similarity of *Anthichnium* and *Dromillopus* Gilmore, 1927, and *Dromillopus parvus* Gilmore, 1927, was subsequently re-assigned to *Batrachichnus* by Haubold *et al.* (1996), highlighting the similarity between *Anthichnium* and *Batrachichnus*. Indeed, Haubold (1998) suggested that *Anthichnium* is synonymous with *Batrachichnus*, and observed that the type specimen of *Anthichnium* is itself an undertrack and therefore not taxonomically stable. *Anthichnium salamandroides* is here accommodated under the ichnosubgenus *Limnopus* (*Batrachichnus*). The ichnotaxon *Anthichnium major*, erected by Haubold and Sarjeant (1973, 1974; BU 3398, Text-fig. 3.3D) to describe *Limnopus* (*Batrachichnus*) trackways of intermediate size from Shropshire, is different from *Limnopus* (*Batrachichnus*) *salamandroides* only in terms of size, not morphology. This ichnospecies is therefore synonymized with *Limnopus* (*Batrachichnus*) *salamandroides*, following numerical analysis of the type specimen. The range of preservational styles within *Limnopus* (*Batrachichnus*) *salamandroides* is variable, dependent upon both trackmaker size and substrate conditions at time of imprinting (Text-fig. 3.3), whereas *L.* (*Batrachichnus*) *plainvillensis* is variable only due to substrate conditions (Text-fig. 3.2).



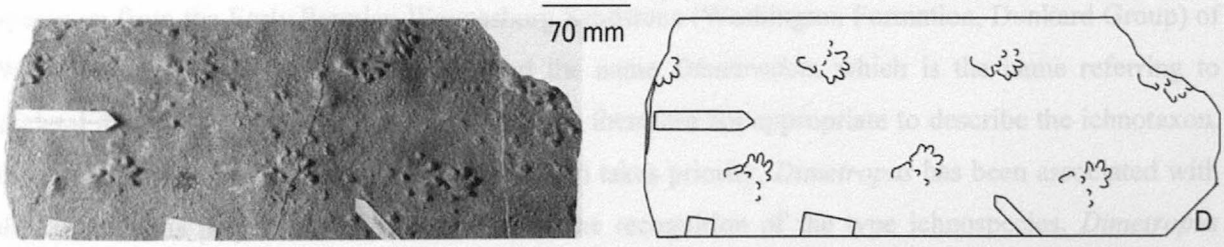
BU 3736



BU 3688



BU 3432a



BU 3398a

TEXT-FIG. 3.3. *Limnopus* (*Batrachichnus*) *salamandroides* (Geinitz, 1861); Alveley Member, Salop Formation, Warwickshire Group. Westphalian D, Shropshire, UK. Selected trackways illustrating range of preservational styles within the ichnospecies. A, BU 3736. B, BU 3688. C, BU 3432a. D, BU 3398a, type specimen of *Anthichnium major* Haubold and Sarjeant, 1973.

Ichnogenus DIMETROPUS Romer and Price, 1940

Type ichnospecies. Dimetrodon berea Tilton, 1931. Early Permian, Waynesburg Sandstone, Washington Formation, Dunkard Group. Berea, Ritchie County, West Virginia, USA. Type specimen WVU Permian Number 147.

Included ichnospecies. Dimetropus leisnerianus (Geinitz, 1863) from the Upper Rotliegend of the Thüringer Wald, Germany; *D. nicolasi* Gand and Haubold, 1988, from the Early Permian of the Lodève and St. Affrique basins, southern France.

Diagnosis. Quadrupedal trackway with pes footlength up to 220 mm. Depending on the stride length, pace angulation 80–100°; stride:footlength ratio averages 3:1 (range 2·5:1 – 4·2:1). Manus and pes long axes lie approximately parallel to the trackway midline. Plantigrade, pentadactyl impression, digit IV longest. Pes heel length comprises over half the total footlength. Digits relatively slender, with sharp, robust claws directed towards the trackway midline. Pes digit divarification between digits I–IV up to 80°, with strongly impressed heel proximal to digits III–V. Manus smaller than pes, total digit divarification (from I–V) 90° on average, with a narrower heel than that of pes. Possible tail trace running straight along trackway midline.

Remarks. Dimetropus was first described by Geinitz (1863), under the name of *Saurichnites leisnerianus*, followed by Pabst (1895), who erected the junior synonym *Ichnium acrodactylum* from the Early Permian (Rotliegend) Tambach Formation of Thüringen, central Germany. The type ichnospecies of *Dimetropus*, *Dimetrodon berea* Tilton, was described by Tilton (1931) based upon a specimen from the Early Permian Waynesburg Sandstone (Washington Formation, Dunkard Group) of West Virginia, USA. However, as he used the name *Dimetrodon*, which is the name referring to skeletal material of the proposed trackmaker and therefore not appropriate to describe the ichnotaxon, the name *Dimetropus* of Romer and Price (1940) takes priority. *Dimetropus* has been associated with the carnivorous pelycosaur *Dimetrodon* since the recognition of the type ichnospecies, *Dimetropus berea* Tilton 1931, based upon comparisons with skeletal material made by Tilton (1931). It was argued by Haubold (1971*a*) that *Dimetrodon* is only one of a number of possible pelycosaurian *Dimetropus* trackmakers, including *Haptodus* and *Sphenacodon*, based upon the skeletal morphology of the manus and pes. Indeed, Haubold and Sarjeant (1973) attributed *D. salopensis* to a sphenacodontid pelycosaur, despite a lack of corresponding Upper Carboniferous body fossils at the time, and this attribution is supported in a recent review of Permian trackmakers by Haubold (2000). The appearance of *Dimetropus* in the Late Carboniferous Alveley ichno-assemblage marks the first occurrence of this ichnotaxon outside the Permian.

Stratigraphical range. Late Moscovian to mid-Kungurian.

Dimetropus leisnerianus (Geinitz, 1863)

Text-figure 3.4

	1863	*Saurichnites leisnerianus* Geinitz, p. 389, pl. 4, fig. 5.
v	1895	*Ichnium acrodactylum* Pabst, p. 575.
* v	1971*a*	*Dimetropus leisnerianus* (Geinitz); Haubold, p. 34.
	1971*b*	*Dimetropus leisnerianus* (Geinitz); Haubold, pp. 32–33, text-fig. 9.
v	1973	*Dimetropus salopensis* Haubold and Sarjeant, pp. 905 – 906, text-fig. 3.2.
v	1974	*Dimetropus salopensis* Haubold and Sarjeant; Haubold and Sarjeant, p. 260, text-fig. 3 (right).
	1973	*Dimetropus leisnerianus* (Geinitz); Haubold, pp. 20–21, pl. 36–39, table 5.
	1982	*Dimetropus leisnerianus* (Geinitz); Fichter, pp. 100–103, text-figs 6–7.
	1983*a*	*Dimetropus leisnerianus* (Geinitz); Fichter, pp. 153–159, text-figs 14A–D, 15.
?	1983*c*	*Dimetropus leisnerianus* (Geinitz); Fichter, pp. 141–142, text-figs 27–28.
?	1984	*Dimetropus leisnerianus* (Geinitz); Fichter, pp. 222–223, text-fig. 15.
p	1987	*Dimetropus leisnerianus* (Geinitz); Gand, p. 167, pl. 6A (*non* 6C), text-figs 47–51, tables 86–92.
	1996	*Dimetropus leisnerianus* (Geinitz); Hunt *et al.*, p. 177, text-fig. 7B.
v	1996	*Dimetropus leisnerianus* (Geinitz); Haubold, pp. 53–54, pl. 14–15, table 6.
	1998	*Dimetropus leisnerianus* (Geinitz); Haubold, p. 10, pl. 5, table 1.
	2000	*Dimetropus leisnerianus* (Geinitz); Haubold, p. 11.

Material. BU 3413; 3434; 3691a; 3706a; 3730a; 3734x.

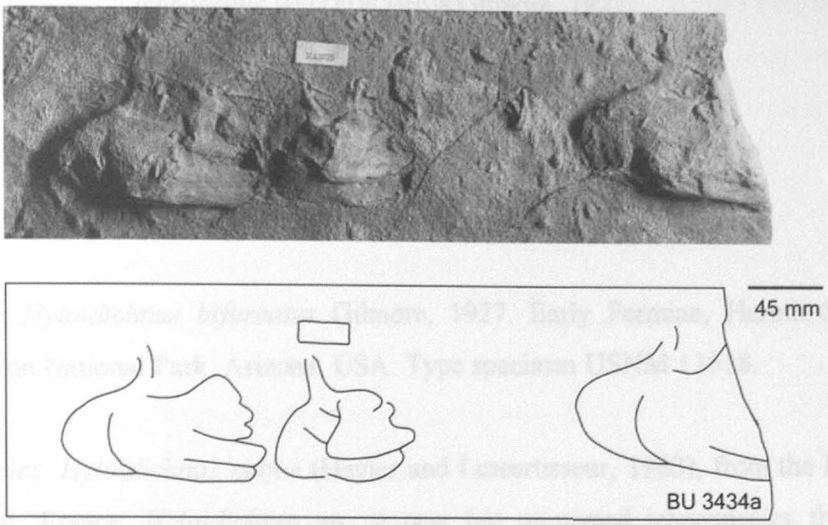
Description

Manus morphology. Pentadactyl, deeply impressed, plantigrade manus 64–66 mm (length) by 41–50 mm (width). Digits long, slender, taper distally. Digits I–III curve slightly laterally; Digit IV lies at 56° (mean) and tip of Digit V curves round medially to lie at 90° with respect to trackway midline. Digit IV is longest, up to 63 mm. Total digit angulation 79°. Broad, rounded heel exhibits deep sole pad, extending from Digits II to V and reaching halfway along sole. Claws may be evident on Digits IV and V, although this is an extra-morphological feature.

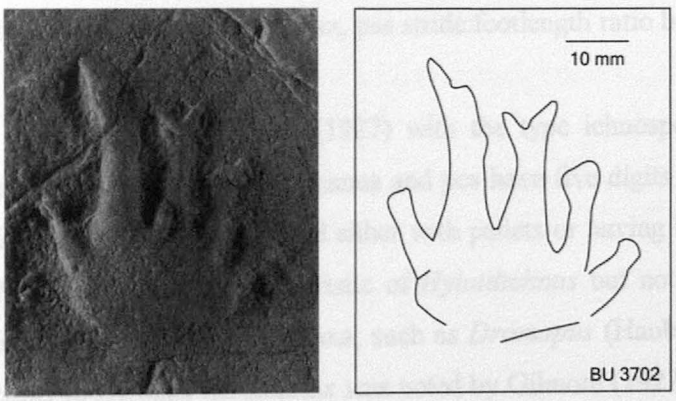
Pes morphology. Pentadactyl, plantigrade pes of length 90–94 mm, width 50–57 mm. Deeply impressed, so that Digits I to II are not distinctly separate. Digits long (II longest, up to 91 mm), slender and distally tapering. Digits I–III slightly laterally curving, Digit IV lies at 40° and tip of Digit V lies at 90° to trackway midline. Mean total digit angulation 66°. Heel broad, elongate, and tapering, with deep, rounded sole pad extending from Digits I–III, reaching halfway along sole. Claws are evident on Digits IV and V. Pes pace measured at 28 mm.

Trackway structure. Manus–pes overlap is variable (1–7 mm). Both manus and pes prints face forwards with respect to trackway midline. Faint, straight tail trace, 10 mm wide, runs at 35 mm from interior extent of manus. Trackwidth (107–132 mm) is approximately three times manus footwidth. Manus stride 92 mm, manus pace 19 mm.

Remarks. Dimetropus leisnerianus was first described by Geinitz (1863) under the name *Saurichnites leisnerianus*, and later by Pabst (1895) under the name *Ichnium acrodactylum*. Whilst the type specimens of *S. leisnerianus* and *I. acrodactylum* appear superficially different, they are now considered to be variants of the trackways of a single type of trackmaker. Haubold (1971*a*) re-assigned *S. leisnerianus* to *Dimetropus*, and drew up a list of criteria with which to identify the new ichnotaxon *Dimetropus leisnerianus*, and a list of possible extra-morphological features. Consequently, *D. leisnerianus* encompasses a large variation within specimens, and includes undertracks. The specimens figured in Fichter (1983*b*, 1983*c*, 1984) are considered to be possible undertracks, although they are not figured sufficiently to enable certain identification. *Dimetropus salopensis* (Haubold and Sarjeant 1973, 1974; Text-fig. 3.4) is here re-assigned to *D. leisnerianus*, as the morphological variance of *D. salopensis* is encompassed by that of *D. leisnerianus*.



TEXT-FIG. 3.4. *Dimetropus leisnerianus* (Geinitz, 1863); Alveley Member, Salop Formation, Warwickshire Group. Westphalian D, Shropshire, UK. BU 3434a, specimen of the type series of *Dimetropus salopensis* Haubold and Sarjeant, 1973. Only the left side of the trackway is preserved.



TEXT-FIG. 3.5. *Hyloidichnus*? *bifurcatus* Gilmore, 1927; Alveley Member, Salop Formation, Warwickshire Group. Westphalian D, Shropshire, UK. BU 3702, isolated pes impression.

Ichnogenus HYLOIDICHNUS Gilmore, 1927

1927 *Hyloidichnus* Gilmore, p. 51–53.
1927 *Hylopus* Gilmore, p. 45–51.
1996 *Gilmoreichnus* Haubold, pp. 33–34.

Type ichnospecies. *Hyloidichnus bifurcatus* Gilmore, 1927. Early Permian, Hermit Shale, Hermit Gorge, Grand Canyon National Park, Arizona, USA. Type specimen USNM 11518.

Included ichnospecies. *Hyloidichnus major* (Heyler and Lessertisseur, 1963), from the Early Permian of Lodève, Herault, France; *Hyloidichnus* sp., a new but un-named ichnospecies from the Early Permian Oberhöf Formation of Friedrichroda, Thüringen, Germany (Haubold, 1971*a*).

Diagnosis (emended from Gilmore 1927; Haubold 1971*a*). Narrow, quadrupedal trackway. Pace angulation over 100° on average, but manus pace angulation higher than pes pace angulation. Partial, primary manus–pes overlap. Both manus and pes impressions pentadactyl and semi-plantigrade with narrow sole. Digit lengths increase I-II-III-IV, V equal to I, digits IV and V usually shallow and incompletely impressed. Digits are straight and slender; digit tips frequently have bifurcated ends (extra-morphological feature). Pes length up to 66 mm, pes stride:footlength ratio between 4:1 and 5:1.

Remarks. *Hyloidichnus* was erected by Gilmore (1927) with the type ichnospecies, *H. bifurcatus*, described as 'quadrupedal, semi-digitigrade. Both manus and pes have five digits. Manus smaller than pes and placed in front of hindfoot. Toes terminated either with pellets or having bifurcated ends'. The bifurcated digit tips of *H. bifurcatus* are characteristic of *Hyloidichnus* but not always present, and may be present on the longer digits of other ichnotaxa, such as *Dromopus* (Haubold *et al.* 1996). The resemblance of *H. bifurcatus* to *Hylopus hermitanus* was noted by Gilmore (1927), and *H. hermitanus* was later selected as the type ichnospecies of *Gilmoreichnus* (Haubold 1971*a*). Subsequent authors (e.g. Haubold 1971*b*) have also recognized the similarity, which had previously led to the 'lumping' of *Hyloidichnus* and *Gilmoreichnus* into a single ichnogenus. Despite claims that *Hyloidichnus* and *Gilmoreichnus* are in fact distinct ichnogenera (e.g. Haubold *et al.* 1995), many authors have assigned specimens of *Hyloidichnus bifurcatus* to *Gilmoreichnus hermitanus*, due to the similarity between these ichnospecies (e.g. Haubold 1971*b*; Haubold *et al.* 1995; Lucas *et al.* 1995). The two ichnogenera are here considered synonymous. Haubold (1971*a*) also noted the similarity between *Hyloidichnus* and the ichnogenera *Amphisauroides* and *Amphisauropus*, and originally attributed these tracks to the Seymouriamorpha stem-amniotes, suggesting that the trackmaker could be any of the biotaxa *Phanerosaurus*, *Diadectes*, *Diasparactus*, *Discosaurus* or *Melanerpeton*. Here, *H. arnhardti* Haubold, 1973, is considered to be a specimen of *Amphisauropus*, after viewing the type specimen. However,

recent work (Haubold 2000) has indicated that *Hyloidichnus* is most likely to have been produced by a representative of a pelycosaurian group, most likely the Eothyrididae, a synapsid group. The appearance of *H. bifurcatus* in the Late Carboniferous Alveley ichno-assemblage extends the known range of *Hyloidichnus* from the mid-Gzelian back into the late Moscovian.

Stratigraphical range. Late Moscovian to Late Artinskian.

Hyloidichnus? *bifurcatus* Gilmore, 1927

Text-figure 3.5

* v	1927	*Hyloidichnus bifurcatus* Gilmore, pp. 52–53, pl. 16, text-fig. 25.
v	1927	*Hylopus hermitanus* Gilmore, pp. 46–51, text-fig. 21, pl. 15.
v ?	1927	*Collettosaurus pentadactylus* Gilmore, pp. 60–63, text-fig. 32, pl. 19, fig. 1.
v	1928	*Hyloidichnus whitei* Gilmore, pp. 5–7, pl. 3, figs 1–2, text-fig. 3.
	1954	'*Procolophonichnium*'? *microdactylum* (Pabst); Müller, pp. 190–195, pl. 16, figs 1–2, text-fig. 1.
v	1971*a*	*Hyloidichnus bifurcatus* Gilmore; Haubold, p. 22, text-fig. 18.9.
v	1971*a*	*Hyloidichnus whitei* Gilmore; Haubold, p. 22, text-fig 18.7 [*kop.* Gilmore 1928, text-fig. 3].
?	1971*a*	*Hyloidichnus major* Heyler and Lessertisseur; Haubold, p. 22, text-fig. 18.8.
	1971*b*	*Varanopus microdactylus* (Pabst 1896); Haubold, pp. 27–28, pl. 7, fig. 2, pl. 17.
	1971*b*	*Gilmoreichnus hermitanus* (Gilmore); Haubold, pp. 33–34, text-figs 20.1, 21A, 22A–B.
?	1971*a*	*Varanopus microdactylus* Moodie; Haubold, p. 30, text-fig. 19.1.
	1971*b*	*Hyloidichnus* sp. nov.; Haubold, p. 24, pl. 2, fig. 2.
	1983*a*	*Varanopus microdactylus* (Pabst); Fichter, pp. 136–147, text-figs 6A–D, 7B, 8A–B, 9A–B.
?	1983*b*	*Hyloidichnus arnhardti* Haubold; Fichter, pp. 97–108, text-figs 68A–B, 69A–B.
p	1987	*Hyloidichnus major* (Heyler and Lessertisseur); Gand, p. 139, pl. 4B, 4D (*non* 4C) text-figs 38–42, tables 66–79.
	1996	*Gilmoreichnus hermitanus* (Gilmore); Haubold *et al.*, pp. 149–154, text-figs 17A–C, 18C.
v	1996	*Hyloidichnus bifurcatus* Gilmore; Lucas *et al.*, p. 273, text-fig. 4D.
v non	1996	*Gilmoreichnus hermitanus* (Gilmore); Lucas *et al.*, p. 273, text-fig. 5C.

	1996	*Hyloidichnus bifurcatus* Gilmore; Hunt *et al.*, p. 296, text-fig. 3C.
v	1996	*Hyloidichnus bifurcatus* Gilmore; Schult, p. 145, text-figs 8A–B, 9A.
v non	1996	*Hyloidichnus bifurcatus* Gilmore; Schult, p. 145, text-fig. 9D.
	1998	*'Varanopus' microdactylus* (Pabst); Haubold, pp. 10–11, text-fig. 6A–C.

Material. BU 3702.

Description

Pes morphology. Pentadactyl, plantigrade pes; square heel of 39 mm wide. Impression strength equal across footprint, with deeper sole pads preserved at digit bases, where digits meet heel. Digits long and slender, with bifurcating tips, an acknowledged extra-morphological feature. Digit lengths increase from I to IV (Digit IV 35 mm in length from hypex to digit tip); Digit V approximately equal in length to Digit I. Digits straight, with total digit angulation of 104°. Footlength 66 mm, footwidth 56 mm.

Remarks. Gilmore (1928) erected *H. whitei* (holotype specimen USNM 11692), from the Hermit Shale of Arizona, based upon the appearance of bifurcated digits upon the manus (*H. bifurcatus* exhibits bifurcated tips only on the pes). However, experiments with modern amphibians and reptiles (Peabody 1959) have shown that this bifurcation is a purely extra-morphological feature, and therefore *H. whitei* is considered to be synonymous with *H. bifurcatus*. Although *H. major* Heyler and Lessertisseur, 1963 is considered to be a separate ichnospecies, the specimen figured by Haubold (1971) is *H. bifurcatus*. The ichnospecies *H. major* was mentioned in a review of Early Permian ichnotaxa by Haubold and Katzung (1972), although it was not formally described by Haubold until 1973.

Ichnogenus ICHNIOTHERIUM Pohlig, 1892

Type ichnospecies. *Saurichnites cottae* Pohlig, 1892. Early Permian, Tambach Formation, Thüringer Wald, Germany. Type specimen GN 1351.

Included ichnospecies. *Ichniotherium rittlerianum* (Hochstetter, 1868), from the Early Permian Braunau Formation of Oslavan and Semil, Czech Republic; *I. aequalis* (Heyler and Lessertisseur, 1963), from the Early Permian of Lodève, southern France; *I. willsi* Haubold and Sarjeant, 1973, from the Late Carboniferous of Alveley, southern Shropshire, UK.

Diagnosis. Quadrupedal trackway with a narrow trackwidth. Depending on the stride length, pes pace angulation 80–135°, with an average value of 90–100°. Stride:footlength ratio normally 3·5:1, with a maximum value of 5:1. Manus impression further turned towards trackway midline than pes. Manus and pes both pentadactyl and plantigrade. Pes and manus digits are robust and sturdy, IV longest, V almost as long. Pes length approximately equal to width, with an oval, inwards extending heel, usually deeply impressed and sharply defined. Pes footlength up to 140 mm. Manus smaller than pes, but relatively broader. Manus sole less strongly defined than heel.

Remarks. *Ichniotherium* has recently been attributed to the Diadectidae (Haubold 2000), following the discovery of diadectid skeletal material in conjunction with the ichnospecies *Ichniotherium cottae* at the Bromacker locality, Thüringen, Germany (Eberth *et al*., 2000). The blunt claws, strong digits and small sole (representative of the carpus) are, however, more characteristic of the Edaphosauria (Haubold 1971*a*). Based upon the foot morphology of *Casea*, *Cotylorhynchus* and *Ennantosaurus*, Haubold (1971*a*) suggested that *Ichniotherium* may have been produced by Early Permian members of the Caseidea, or Edaphosauria. However, the most recent attribution of *Ichniotherium* to *Diadectes* will be followed here. *I. willsi* was possibly produced by a primitive, Carboniferous form of the trackmaker that produced the Lower Permian type ichnospecies *I. cottae* Pohlig 1892 (Haubold and Sarjeant 1973). This statement is based upon the less integrated sole morphology of the former ichnospecies.

Stratigraphical range. Late Moscovian to mid-Kungurian.

Ichniotherium willsi Haubold and Sarjeant, 1973

Text-figure 3.6

v * 1973 *Ichniotherium willsi* Haubold and Sarjeant, pp. 900–904, text-fig 3.1.

v 1974 *Ichniotherium willsi* Haubold and Sarjeant; Haubold and Sarjeant, p.262,

text-fig. 3 (left).

Material. BU 2471a; 3703a.

Diagnosis. Ichnospecies of *Ichniotherium* that is plantigrade with an elongate, laterally extended sole bearing small, deep pad. Sole in two sections, the first extending from the digits I to IV, the second extending from digit V.

Description

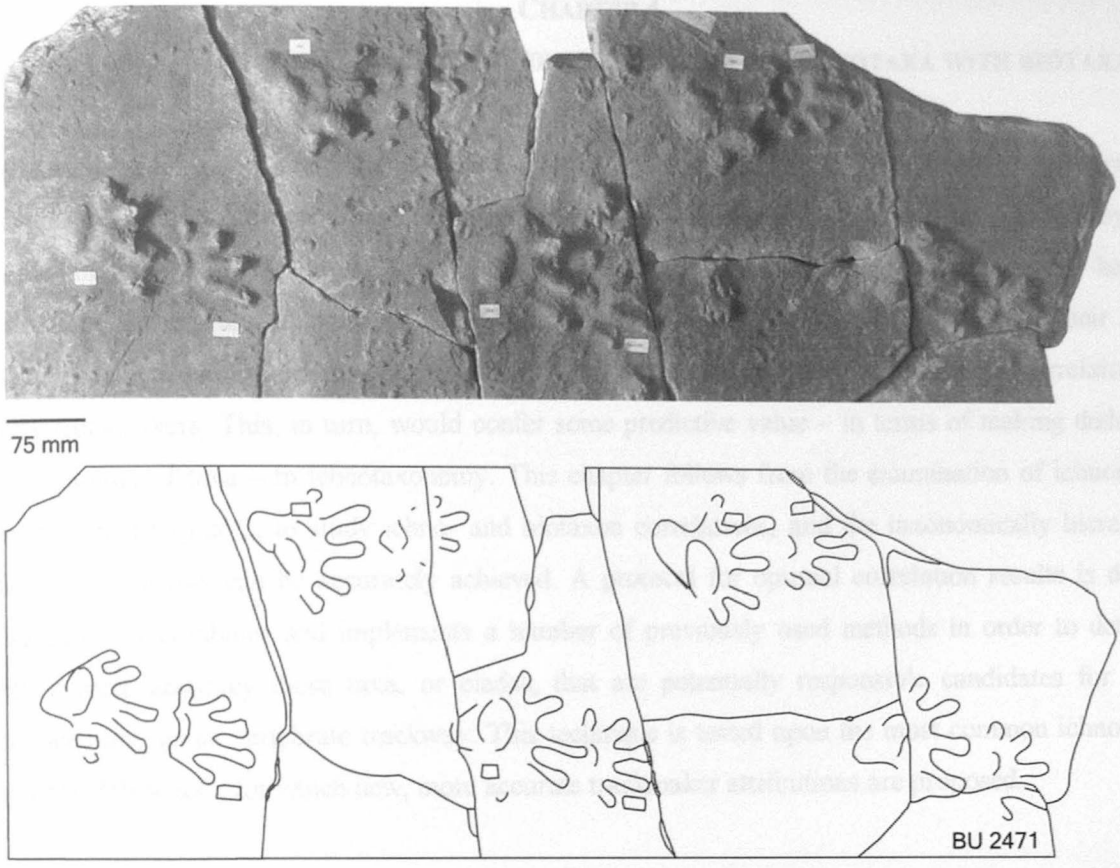
Manus morphology. Pentadactyl, plantigrade manus with slight increase in impression strength distally along digits. Digits II, III and IV deeply impressed – especially at base where digits meet sole; I and V fainter. Digits straight, relatively long in proportion to footlength (75–83 mm, footwidth 78–96 mm), tips enlarged. Longer digits (IV longest, up to 49 mm from hypex to digit tip) appear slender, whilst shorter digits appear broader, as digit breadth remains fairly consistent (8–15 mm at digit bases). Some digits show very faintly defined phalanges. Mean total digit angulation 141° (range 126–152°). Sole characterized by lunate pad at base of digits, curving convexly towards digit tips. No other sole pads impressed, heel obscured by overlapping pes. Heel 23–45 mm long, 23–28 mm wide.

Pes morphology. Pentadactyl, plantigrade pes. Impression strength greater than manus; also larger than manus (footlength 121–128 mm, footwidth 91–95 mm). Digits short in proportion to footlength, broad and straight, tips enlarged. Digit V often represented only by enlarged tip. Digit III longest (up to 43 mm from hypex to digit tip). Mean total digit angulation 86°, range 80–93°. Deep imprinting of digits gives impression of intra-digital webbing. Although this is consistent throughout the trackway, it is likely to be an extra-morphological feature. The presence of claws suggested by ridged, sloped imprint at front of each digit tip, although this may also be an extra-morphological feature. Sole is marked by large, oval pad, placed halfway down sole, width approximating to footwidth, impressed as deeply as digit tips. Remainder of sole elongate with rounded heel, laterally inclined, faintly imprinted. Heel length 84–87 mm, heel width 16–18 mm.

Trackway structure. Distance between manus and pes varies throughout trackway length, with maximum overlap value of 12 mm; maximum distance between manus heel and pes digit III tip 14 mm. Trackwidth very low in comparison to footlength (manus trackwidth 177–192 mm, pes trackwidth 158–174 mm), mean interior trackwidth – 75 mm – measures less than mean pes width of 93 mm, with relatively high stride:trackwidth (mean manus value 2·0, mean pes value 2·3). Manus prints forward facing or medially inclined (manus print angulation 80–87°), pes prints laterally inclined (pes print angulation 97–104°). Manus pace angulation 91–94 mm, pes pace angulation 94–

111 mm. Manus stride 372–385 mm, manus pace 309–312 mm, stride:footlength 4·5 to 4·8. Pes stride 392–395 mm, pes pace 244–270 mm.

Remarks. Ichniotherium willsi shows considerable morphological differences from *I. cottae* of the Early Permian of Germany. Digit arrangement and heel shape vary considerably between the two ichnospecies. Although the characteristic extension to the heel seen in *I. willsi* is seen on a small number of specimens of *I. cottae* (e.g. MNG 1983) from the Early Permian Tambach Formation of Germany, the heel of *I. willsi* extends to a much greater extent. Whilst this may be a purely extra-morphological feature, the difference in amount of extension is such that *I. willsi* is not considered to be synonymous with *I. cottae*.



TEXT-FIG. 3.6. *Ichniotherium willsi* Haubold and Sarjeant, 1973; Alveley Member, Salop Formation, Warwickshire Group. Westphalian D, Shropshire, UK. A, BU 2471.

CHAPTER 4

TRACKWAYS MEET TRACKMAKERS: THE CORRELATION OF ICHNOTAXA WITH BIOTAXA

Vertebrate trackways are often underestimated as a source of data regarding terrestrial palaeocommunities. However, they can provide a lot of information that cannot be supplied by body fossils including, for example, aspects of behaviour, locomotory systems, preferred habitats, community structure, and possible taxon interactions, such as predation. Nevertheless, their use in palaeobiological studies would be greatly increased if trackways could be accurately correlated with likely trackmakers. This, in turn, would confer some predictive value – in terms of making deductions about biological taxa – to ichnotaxonomy. This chapter follows from the examination of ichnospecies concepts in Chapter 2, to study ichno- and biotaxon correlations, and the taxonomically hierarchical level to which this can be accurately achieved. A protocol for optimal correlation results is devised. This protocol combines and implements a number of previously used methods in order to determine with greater accuracy those taxa, or clades, that are potentially responsible candidates for having produced any given vertebrate trackway. This technique is tested upon the most common ichnotaxa of the Late Palaeozoic, for which new, more accurate trackmaker attributions are proposed.

The correlation of ichnotaxonomy with biotaxonomy

The amount of information yielded by trace fossils is greatly increased if considered in conjunction with skeletal material. This requires the reconciliation and correlation of phenetic ichnotaxonomy with phylogenetically determined biotaxonomy. This has previously been most frequently attempted using direct comparison of trackways with skeletal material (e.g. Haubold 1971*a*, *b*, 1996, 1998, 2000; Schult 1995*a*; Haubold and Lucas 2001), and with modern salamander trackways (Peabody 1959; Brand 1979, 1996). However, as noted by Schult (1995*a*), few articulated manus and pes skeletons appear in the Palaeozoic fossil record due to their delicate construction. Therefore, direct comparisons are not always feasible, and many authors rely upon 'personal experience and general rules of thumb' (Schult 1995*a*, p. 123), such as the presence of short, stubby digits in amphibians and pointed, clawed digits in reptiles. As a result, identifications of trackmakers may be rather subjective and not particularly accurate. Farlow and Lockley (1993) improved upon this situation using numerical methods for trackway-trackmaker correlation purposes, comparing phalangeal length ratios of tridactyl dinosaur footprints with those of suitable trackmaker candidates. Their method distinguishes theropods, hypothetically advanced tridactyl prosauropods, and bipedal ornithischians, but relies upon the presence of clear, well-preserved digital nodes, or landmarks. In the absence of such nodes, the level of correlation is reduced, and 'bipedal dinosaur' becomes the most appropriate attribution. It appears then, from all research to date, that Haubold's (1984) claim that a vertebrate ichnospecies is approximately equivalent to a skeletal genus is unfounded. Consequently, an approach that systematically identifies monophyletic clades, which qualify as potential trackmakers, and

distinguishes the most likely trackmaker taxa within these clades, is required. This can potentially be achieved using a method first outlined by Olsen (1995), who stated that 'ichnotaxa can be assigned to biological taxa only if they have shared derived characteristics of those taxa' (Olsen 1995, p. 86). Carrano and Wilson (2001) supported that proposal, and carried out an analysis of the Dinosauria, identifying synapomorphies that relate to features distinguishable in trackways at varying levels of preservation. The same study expanded upon the ideas of Olsen by using additional trackway features that may help resolve trackmaker identity, for example, body size, stratigraphical age, and geographical provenance. It was also noted that 'ichnological studies would benefit from a more explicit articulation of which hierarchical level is appropriate and attainable' (Carrano and Wilson 2001, p. 572). This study investigates and develops this method, providing a systematic approach to trackmaker identification, and thereby examines the hierarchical taxonomic level to which Late Palaeozoic trackways and trackmakers can be correlated.

Aims

This study focuses on Late Palaeozoic terrestrial tetrapod ichnology, and surveys the general principles and goals of ichnology in general. The main aims are as follows:

1. To investigate an accurate method of determining trackmaker identities using selected trackway features.
2. To distinguish the hierarchical level to which trackways can be correlated with trackmaker groups.
3. To facilitate comparison of trace fossils with skeletal assemblages. This study, in particular, aims to illustrate how Late Palaeozoic trackway data can be utilised in conjunction with skeletal data, thereby increasing depth of knowledge in this field. This is especially important as firstly, trackway data give information that is not necessarily available from skeletal material, for example, behaviour, locomotory style and preferred habitats (as trackways are definitely *in situ*), and secondly, the different conditions favouring the preservation of body and trace fossils means that trackways are infrequently found in conjunction with skeletal material, so the two can provide independent sources of palaeobiological information.
4. Following from the above, to enable more accurate palaeoecological reconstructions of ichnological assemblages.

Trackway-trackmaker correlation

In order to utilise as much information as possible to narrow down possibilities of trackmaker identities, a combination of three correlation methods are used. Carrano and Wilson (2001) identified and discussed various methods of trackway-trackmaker correlation, and the hierarchical levels to which certain trackmakers and trackways can be equated. The protocol employed here ensures the

maximum resolution of trackway-trackmaker correlation, and reduces the subjectivity involved in the process. The recommended steps are as follows:

1. Synapomorphy-based correlation. This links trackways to trackmakers using shared derived characters of biotaxa that are identifiable in trackways. These are restricted predominantly to the appendicular, and occasionally to the axial, skeleton. Examples include manus and pes digit number, and the presence of pedal claws (e.g. in theropods). The use of synapomorphies ensures the highest level of confidence in correlations and should therefore always be undertaken before other methods of correlation are applied. This method of correlation is the only means by which potential trackmakers can, without reservation, be excluded from consideration. Obviously, only known taxa are taken into account, but as new taxa are discovered and cladograms potentially alter, correlated ichnotaxa change accordingly, and should not remain associated with obsolete group names.

2. Phenetic correlation. This involves the use of autapomorphies, or derived characters uniquely possessed by a single biotaxon, together with characteristics not regarded as autapomorphies but nevertheless distinctive within a restricted number of particular groups. These morphological features give information that precludes a certain biotaxon, or group of biotaxa, from having produced a certain trackway. Examples of such characters are: very small body size in microsaurs and millerettids; aquatic mode of life in nectrideans and mesosaurs; greater than 60 presacral vertebrae in the lysorophid *Brachydectes*; flight adaptations in *Coelurosauravus*; reduced feet size in the Caseidae. In addition, manus and pes morphologies as indicated by body fossils are compared with trackway morphologies to indicate the closest 'match'.

3. Coincidence correlation. The most likely trackmakers from the remaining list of potential candidates are identified, based upon the assumption that biotaxa with similar stratigraphic ranges to the trackway under consideration are most likely to be the producers of this trackway. The possibility of a trackway representing an extension of the range of a known body fossil is not disregarded but where this is unfeasible, or very unlikely, biotaxa of a corresponding age are preferred to those requiring a range extension. Comparisons with biotaxon frequencies at other sites are made, and the most abundant biotaxa at sites of the same stratigraphical age and environment are suggested as the most likely trackway producers, in preference of more rare forms. Rarely, coincidences of occurrence occur that, unaccompanied, lead trackways to be assigned to certain trackmakers in preference of other groups. For example, at the Bromacker locality in Tambach, central Germany, high frequency co-occurrences of *Ichniotherium cottae* and the potential trackmaker *Diadectes* have led

authors to believe that the two taxa are associated (Eberth *et al.* 2000; Voigt 2001). However, the recent discovery at Tambach of a new, as yet undescribed diadectid genus (Berman *et al.* 2000, Berman and Henrici, 2003) has cast doubt upon this assignation. As noted above, the preservation of body fossils and trackway material is often favoured by dissimilar conditions. Consequently, trackways may represent the traces of different, perhaps undiscovered, biotaxa from those found at skeletal sites of the same age and environment. Coincidence correlation cannot therefore be relied upon to provide an accurate answer, but merely an evidence-based estimation.

A case study: the trackmaker of *Limnopus*

The ichnogenus *Limnopus* Marsh, 1894, is common across both Europe and North America, with a stratigraphical range from the Late Carboniferous (Moscovian) to Late Permian (Tatarian). Some of the most significant records of occurrences include: Geinitz 1861; Marsh 1894; Woodworth 1900; Pabst 1908; Lull 1918; Gilmore 1927; Baird 1952; Haubold 1970, 1971*a*, 1996, 2000; Lucas and Heckert 1995; a full systematic review is given by Tucker and Smith (in press; Chapter 3). The ichnogenus comprises two ichnosubgenera, *Limnopus* and *Batrachichnus*, distinguished only by size differences, but which are thought to have been produced by different trackmakers, as suggested by their different stratigraphical ranges (Tucker and Smith in press; Text-fig. 1.14). *L.* (*Limnopus*) has been most recently attributed to the biogenus *Eryops* (Haubold 2000), a taxon interpreted as a stem-lissamphibian in the analyses of Milner (1988), Milner and Sequeira (1994), and Ruta *et al.* (2003).

Some information regarding the identity of potential *L.* (*Limnopus*) trackmakers can be ascertained from the trackway. For example, *L.* (*Limnopus*) represents an animal with terrestrial abilities, with a tetradactyl manus and pentadactyl pes. The position of the manus with regard to the pes indicates that body length is approximately equal to stride length, and pes digit lengths increase in the order I-II-III-IV, with V equal to II. Text-fig. 4.1 gives a full list of features. The ichnogenus is used here to demonstrate the use of the above methods, and to examine the hierarchical taxonomic level to which Late Palaeozoic trackmakers and trackways can be correlated. In particular, this study aims to determine whether attribution to a generic level biotaxon, as noted above, is justifiable.

In order to constrain the analysis to a workable level, it is considered reasonable to assume that the Late Palaeozoic trackways were produced by Late Palaeozoic trackmakers. Using the combined, adapted early tetrapod phylogenies of Reisz (1986), Laurin (1993), Gauthier (1994), Laurin and Reisz (1995), Lee (1995), and Ruta *et al.* (2003), synapomorphies of Late Palaeozoic biotaxa associated with the appendicular and axial skeleton, which may be identifiable in trackways, were determined (Text-fig. 4.2; Appendix 4). Care was taken to utilise only those trackway features directly related to trackmaker anatomy; extra-morphological features resulting from varying substrate conditions are not

appropriate for use in trackmaker identification, as they do not directly reflect trackmaker morphology. Ideally, in the same way that ichnotaxonomy should be based upon well-preserved, surface level trackways (Tucker and Smith in press), the latter material alone should be used to identify potential trackmakers and the results applied to less well-preserved material subsequently.

Due to the high degree of disarticulation and disruption caused by transport of delicate tetrapod manus and pes bones, there are currently few recognised synapomorphies applicable for this study (Appendix 4). However, recent studies (Laurin 1998) have demonstrated that manus dactyly is an important character in early vertebrate phylogenies (Text-fig. 4.2). The earliest limbed vertebrates, the stem-Tetrapoda, exhibit polydactyly in both the manus and pes. For example, *Acanthostega* has a manus digit count of eight (Coates 1996), whilst in the slightly more derived *Tulerpeton*, this figure is reduced to six (Lebedev and Coates 1995). Pentadactyly can arguably be accepted as the derived state in early crown-group tetrapods (Laurin 1998, Clack 2002*a*). A limited number of Late Palaeozoic tetrapods are tetra- or tridactylous in the manus, including the Microsauria, and the paraphyletic group 'temnospondyli', regarded by many as the ancestors of the recent Lissamphibia (e.g. Milner and Sequeira 1994; Ruta *et al.* 2003).

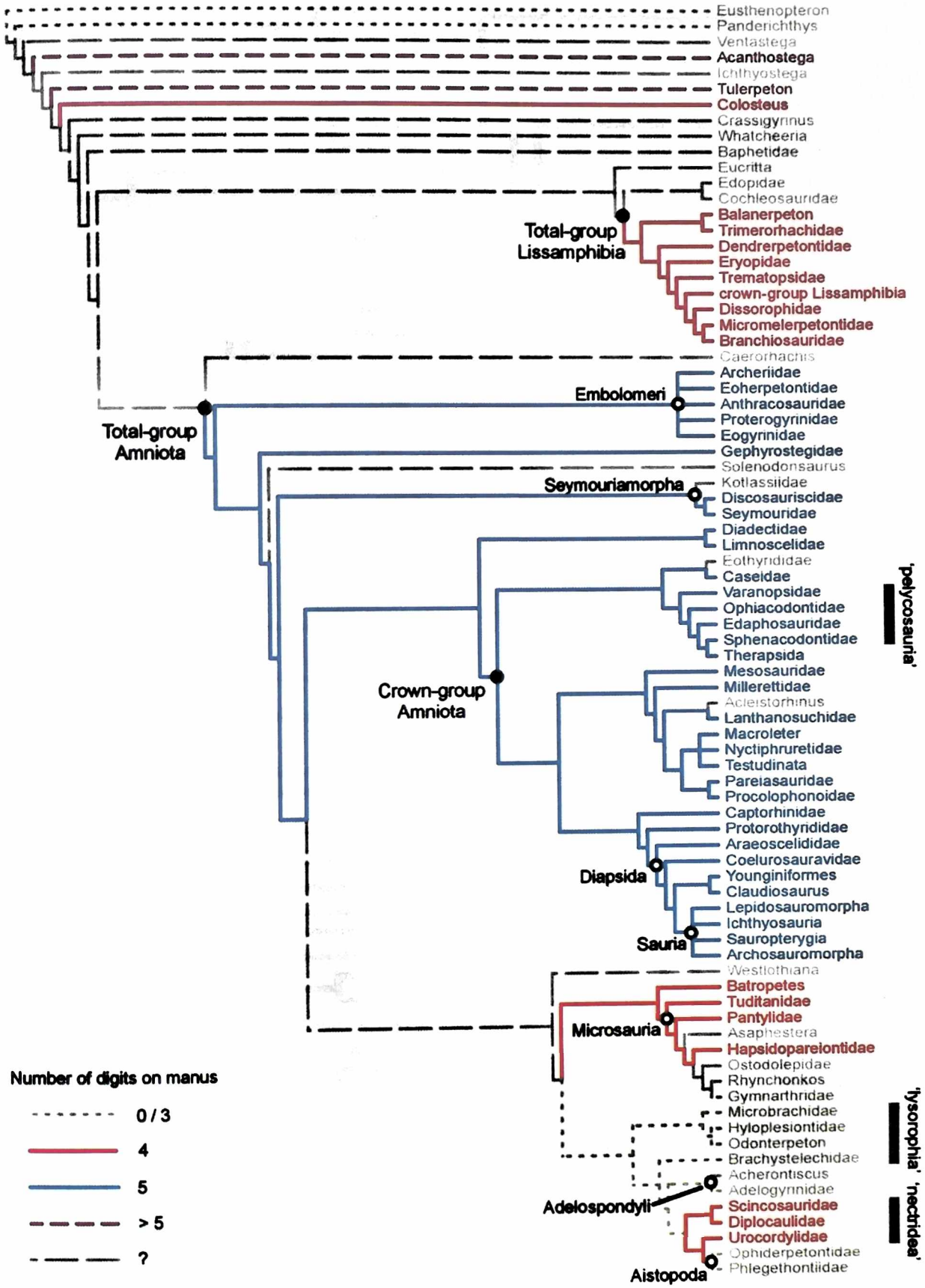
The correlation of Late Palaeozoic trackmakers and trackways is thus strongly constrained by manus dactyly. Any given trackway could theoretically have been produced by any biotaxon exhibiting the same number of digits in the manus as is found in the trackway. For example, trackways of the ichnogenus *L.* (*Limnopus*), which exhibits a tetradactyl manus, could only have been produced by Late Palaeozoic trackmakers possessing a manus with four digits; in other words, the stem-Lissamphibia, ('temnospondyli'), Microsauria, nectridea, and *Colosteus* (Text-fig. 4.2). Although this eliminates the majority of Late Palaeozoic trackmaker taxa, it is evident that *L.* (*Limnopus*) cannot be attributed to any single group of taxa on this character alone, let alone to a taxon at generic level, as suggested by Haubold (2000). However, some taxa within the remaining groups can be discounted following phenetic and coincidence correlation (Text-fig. 4.3). For instance, fully aquatic forms, such as *Isodectes*, *Colosteus*, and all nectrideans apart from *Scincosaurus*, can be discounted from the list of potential trackmakers, together with those taxa exhibiting a particularly long presacral vertebral column (Text-fig. 4.3A). Those forms that exhibit large differences in relative manus and pes digit lengths in comparison to those ratios in *L.* (*Limnopus*), (manus longest digit length: pes longest digit length ratio of 1:1.3), for example, *Dendrerpeton* (manus longest digit length: pes longest digit length ratio of 1:1.9; Text-fig. 4.3.B) can also be removed. Text-figure 4.3C illustrates the taxa that can be eliminated from the list of potential trackmakers using all available criteria, and demonstrates that *L.* (*Limnopus*) can, through phenetic and coincidence correlation, be assigned with some certainty to the stem-Lissamphibian temnospondyls. This assignation is supported by the comparison of *L.* (*Limnopus*) manus and pes outlines with reconstructed skeletal morphologies of typical stem-lissamphibians and

microsaurs (Text-fig. 4.4). However, even with the use of further phenetic and coincidence correlatory criteria (Text-fig. 4.1), *L.* (*Limnopus*) cannot be attributed to any single biogenus. It can nevertheless be said that *L.* (*Limnopus*) is the trace of a stem-lissamphibian, which remains a useful determination, in particular for palaeoecological studies. A higher level of biotaxonomic appropriation is not possible.

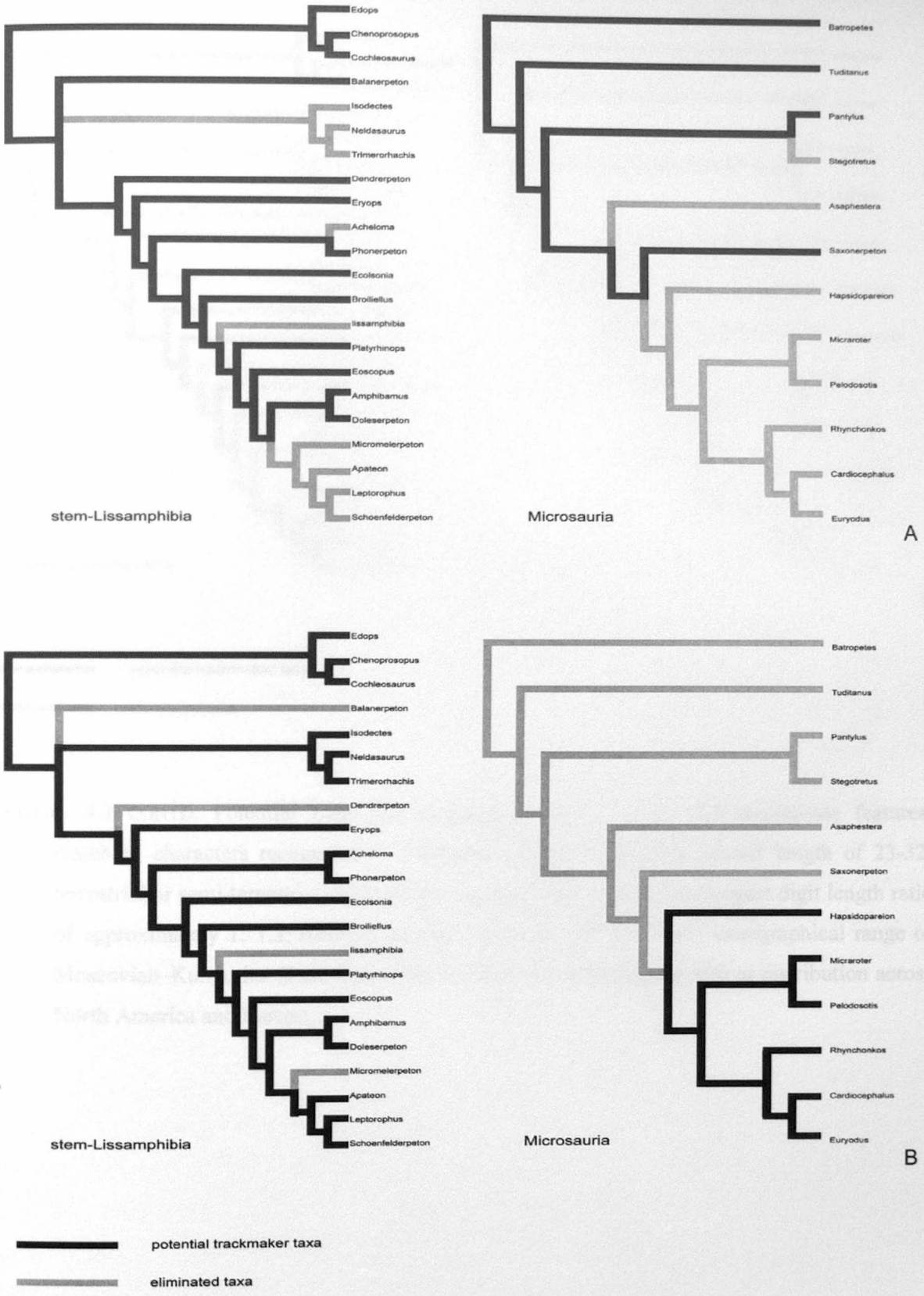
***Limnopus* (*Limnopus*) *vagus*:**

Geographical Distribution	Stratigraphical range	Previous biotaxon assignations	Significant ichnological features with related osteological synapomorphies	Other significant ichnological features
North America, Europe	Late Moscovian to Late Tatarian (Late Carboniferous to Late Permian)	Edopsoidea or Eryopoidea (Haubold 1971); *Eryops* (Haubold 2000)	Quadrupedal trackmaker; tetradactyl manus	minor manus-pes overlap indicating relatively short body length / presacral vertebral column; manus longest digit to pes longest digit ratio of 1: 1.3; manus slightly smaller than pes and inturned towards trackway midline, indicating sprawling gait; footwidth greater than footlength; manus digits short and broad with rounded tips, pes digits long and slender; digit lengths increase I-IV-II-III (manus) and I-II-III-IV, V=II (pes); relatively low pace angulations.

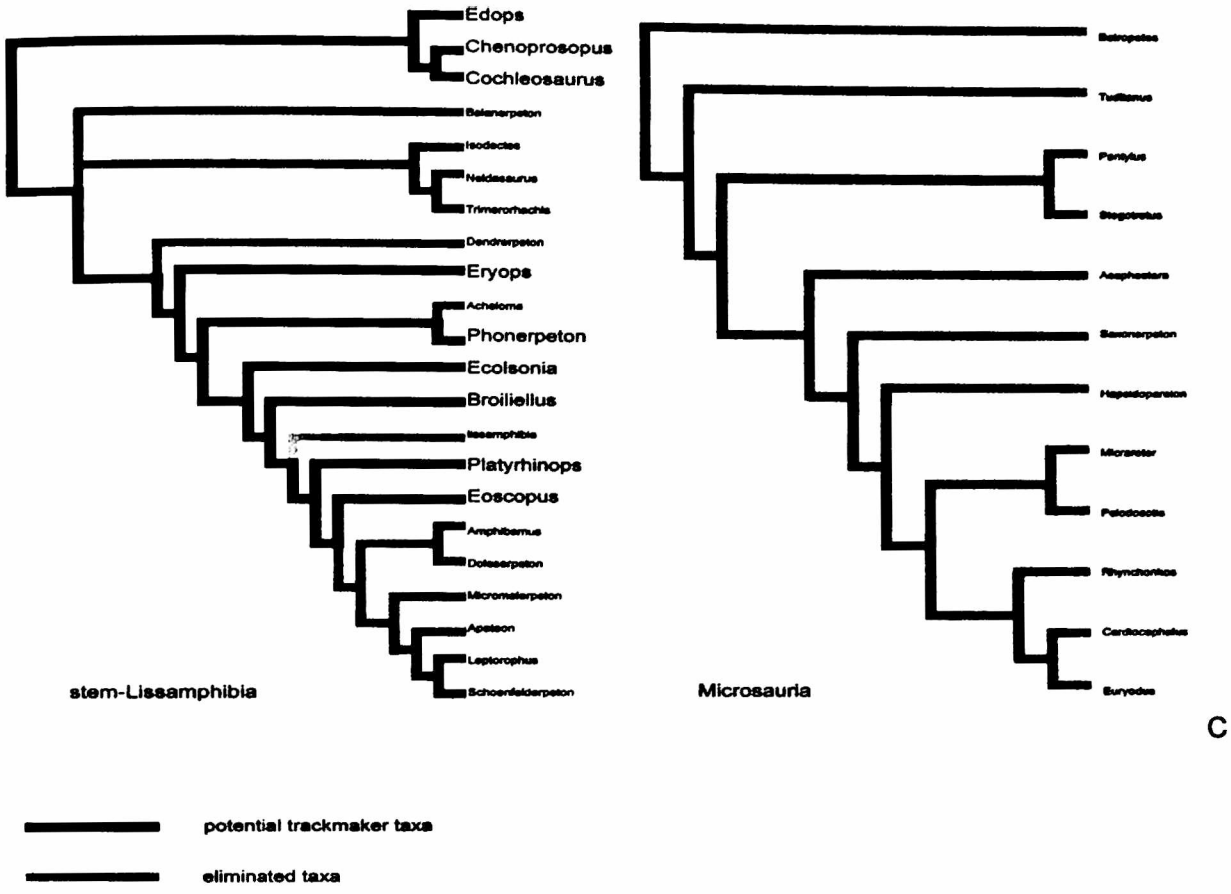
TEXT-FIG. 4.1. Trackway features of *Limnopus* (*Limnopus*) that give information about the identity of potential trackmakers. Data from Tucker and Smith (in press; Chapter 3).



TEXT-FIG. 4.2. The evolution of manus dactyly in early tetrapods. Phylogeny from Reisz (1986), Laurin (1993), Gauthier (1994), Laurin and Reisz (1995), Lee (1995), and Ruta *et al.* (2003).

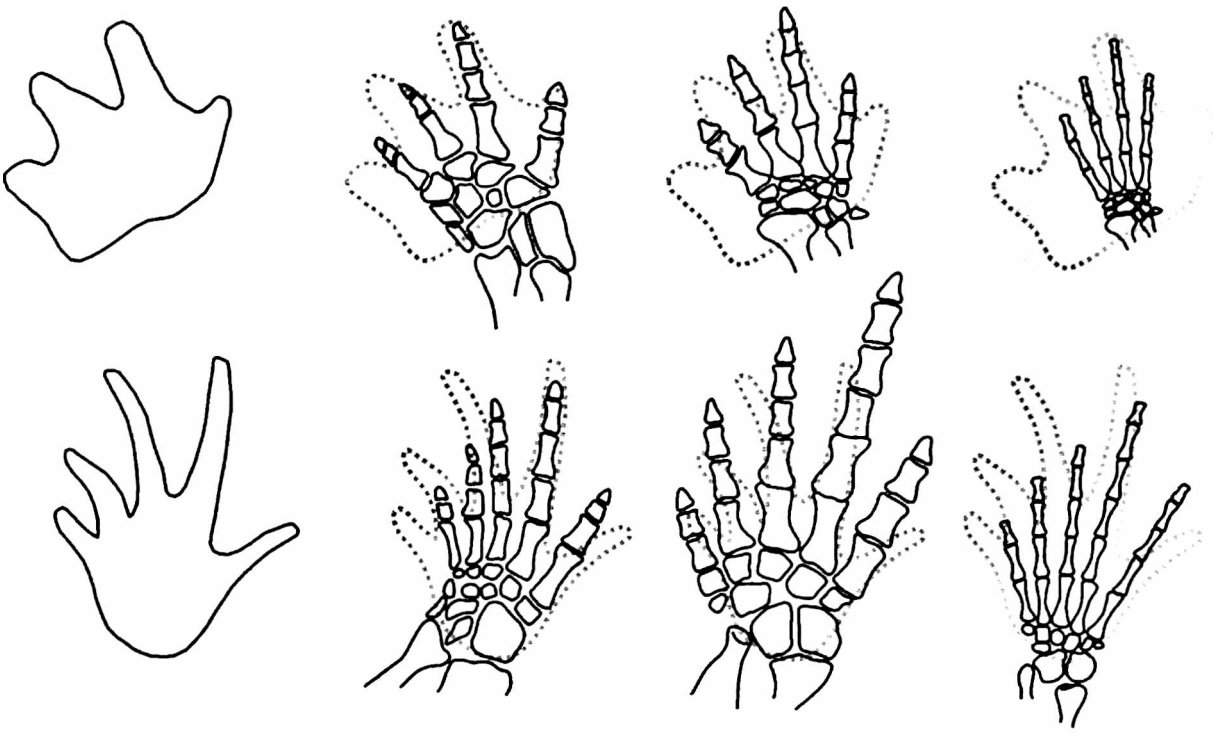


TEXT-FIG. 4.3. Potential *Limnopus* trackmaker taxa. Crown-group Lissamphibia have an inappropriate stratigraphical range and are already eliminated. A, Taxa with an appropriate presacral vertebral column length (taken as a proxy for body length), and an appropriate mode of life. B, Taxa with an appropriate manus longest digit to pes longest digit length ratio.



C

TEXT-FIG. 4.3 CONTD. Potential *Limnopus* trackmaker taxa. C, Taxa with appropriate features, matching characters recognised in *Limnopus*: presacral vertebral column length of 23-32; terrestrial or semi-terrestrial mode of life; manus longest digit to pes longest digit length ratio of approximately 1: 1.3; medium average body size (up to 1.5 m); stratigraphical range of Moscovian–Kungurian (Late Carboniferous–Early Permian); geographical distribution across North America and Europe.



TEXT-FIG. 4.4. Shape comparison of manus and pes of *Limnopus* (*Limnopus*) with reconstructed skeletal morphologies of typical microsaurs (*Pantylus*, *Saxonerpeton*, *Tuditanus*; Carroll and Gaskill 1978) and a stem-lissamphibian (*Eryops*; from reconstructed skeletal material at the Smithsonian Institution, Washington, USA). *L.* (*Limnopus*) outline of a typical manus-pes set from the Late Carboniferous Alveley Member, Shropshire, UK. Not to scale.

The identity of other Late Palaeozoic trackmakers

Using the methodology outlined above it is possible to determine the trackmakers of other Late Palaeozoic ichnotaxa. Late Palaeozoic trackway assemblages across Europe and North America exhibit a conservative, cosmopolitan ichnofauna, consisting predominantly of the ichnotaxa *Amphisauropus*, *Dimetropus*, *Dromopus*, *Hyloidichnus*, *Ichniotherium* and *Limnopus* (*L.* (*Limnopus*) and *L.* (*Batrachichnus*)). Taxa such as *Chelichnus*, and *Erpetopus* or *Varanopus* may be present, depending upon the quality and extent of preservation, and depositional environments.

Amphisauropus Haubold, 1970

Type ichnospecies: *Amphisauropus latus* Haubold, 1970.

Other included ichnospecies: *A. imminutus* Haubold, 1970.

Synonymous ichnogenus: *Pachydactylichnia* Pabst, 1900.

***Known stratigraphical range*:** Asselian to Kazanian (Early–Late Permian).

***Known geographical distribution*:** Thüringen, Germany; Provencal Basins, France; Sachsen and Dolny Slask, Poland; Russia; N. Italy; New Mexico, USA.

***Characters of trackways*:** quadrupedal; pentadactyl manus and pes; plantigrade to semi-plantigrade impressions; hand smaller than foot; manus digit lengths from I-II-IV-III, V=I, pes from I-II-III-IV, V~II; primary coupling; manus inturned, pes aligned with midline; pes digit length ratios of 1.5, 1.2, 1.3, 0.6; manus digit length ratios of 1.3, 1.1, 1.1, 0.6; manus longest digit to pes longest digit ratio of 1.4–2.0.

***Previous attributions*:** Seymouriamorpha, perhaps *Phanerosaurus*, *Diadectes*, *Diasparactus*, *Discosauriscus*; or *Melanerpeton* (Haubold 1971*a*); *Diadectes* (Haubold 1971*b*); Eryopoidea or Diadectidae (Haubold 1996); Seymouriamorpha (Haubold 2000).

New attributions: The most likely trackmaker candidates for *Amphisauropus* are the Seymouriidae, a stem-amniote taxon within the Seymouriamorpha (= Seymouridae; Kotlassiidae; Discosauriscidae). This is based upon the similar manus and pes digit length ratios, a similar stratigraphical range, and the bluntly rounded unguals and appropriate body proportions and size of seymouriids.

Chelichnus Jardine, 1850

Type ichnospecies: *Chelichnus duncani* (Owen, 1842).

Other included ichnospecies: A number of other species of *Chelichnus* have been erected, however, none of these are considered to be valid by the present author, as they represent variation in extra-morphological features rather than diversity in trackmaker anatomy.

Synonymous ichnogenera: *Testudo* Owen, 1842; *Laoporus* Lull, 1918; *Agostopus* Gilmore, 1926; *Barypodus* Gilmore, 1926; *Palaeopus* Gilmore, 1926.

***Known stratigraphical range*:** Artinskian to Kungurian (Mid-Permian).

***Known geographical distribution*:** Central Germany; northern England; Scotland; Arizona, Colorado, USA.

***Characters of trackways*:** quadrupedal; pentadactyl manus and pes in well preserved tracks; characterised by shortened, rounded impressions, often with raised crescent at base of heel (an extra-morphological feature created by slumping of sandy, unconsolidated substrate). Trackway pattern is variable, although stride lengths and trackway widths are often relatively low.

***Previous attributions*:** Synapsid (Haubold *et al.* 1995*b*; Lockley *et al.* 1995; Haubold 1996); caseid 'pelycosaur' (Baird 1952; McKeever 1994; Kramer *et al.* 1995); caseid, perhaps *Casea*, *Cotylorhynchus*, *Angelosaurus* or *Ennatosaurus* (Haubold 1971*a*); "anomodont- or pareiasaur-like animals" (McKeever 1991).

New attributions: *Chelichnus* is an ichnogenus highly controlled by sedimentary facies, and its morphology is little affected by trackmaker anatomy. The author considers this a form genus, applied to trackways made within unconsolidated, sandy substrates. In some cases, the outline of five digits may be apparent, suggesting an amniote trackmaker, but the morphology of these remains strongly affected by substrate conditions, and thus no further correlation is appropriate.

Dimetropus Romer and Price 1940

Type ichnospecies: *Dimetropus berea* (Tilton, 1931).

Other included ichnospecies: *D. leisnerianus* (Geinitz, 1863); *D. nicolasi* Gand and Haubold, 1988.

Synonymous ichnogenera: *Akrodactylichnium* Pabst, 1895; *Akrodactylichnia* Pabst, 1900; *Pachydactylichnia* Pabst, 1900; *Dimetrodon* Tilton, 1931.

***Known stratigraphical range*:** Bashkirian to Kazanian (Mid-Carboniferous–Late Permian)

***Known geographical distribution*:** Provencal Basins, France; Thüringen, Germany; western Dolomites, northern Italy; Sachsen, Dolny Slask, Poland; Russia; Shropshire, UK; Alabama, Arizona, Colorado, New Mexico, Ohio, Texas, West Virginia, USA.

***Characters of trackways*:** quadrupedal; pentadactyl manus and pes; relatively large size (up to 220 mm); stride:footlength ratio averages 3:1; manus and pes aligned with trackway midline; pes heel length comprises over half total pes footlength; relatively slender digits; strongly impressed heel proximal to digits III-V; manus smaller than pes; straight tail trace; plantigrade impression; digit lengths increase from V-I-II-III-IV (manus), I-II-III-V-IV (pes); manus longest digit to pes longest digit ratio of 1.2; pes digit length ratios of 1.2, 1.3, 1.4, 0.7; manus digit length ratios of 1.1, 1.3, 1.2, 0.4; manus to pes longest digit length ratio of 1.3.

***Previous attributions*:** *Dimetrodon* (Tilton 1931); *Dimetrodon*, *Haptodus* or *Sphenacodon* (Haubold 1971*a*, *b*); sphenacodontid 'pelycosaur' (Haubold 1996, 1998, 2000; Haubold and Sarjeant 1973).

New attributions: Ophiacodontidae, a 'pelycosaurian' group with the Synapsida. The reasons for this attribution, other than shared synapomorphic characteristics (e.g. pentadactyl manus and pes), include the similar stratigraphical range, appropriate recorded sizes of ophiacodontids, and the digit length and manus-pes size ratios of *Ophiacodon*, which correlate very well with those of *Dimetropus*.

Dromopus Marsh, 1894

Type ichnospecies: Dromopus agilis Marsh, 1894.

Other included ichnospecies: D. lacertoides (Geinitz, 1861); *D. palmatus* (Moodie, 1929).

Synonymous ichnogenera: Gampsodactylichnia Pabst, 1900; *Tanydactylichnia* Pabst, 1900; *Eumekichnium* Nopsca, 1923; *Gampsodactylum* Nopsca, 1923.

Known stratigraphical range: Kasimovian to Kazanian (Late Carboniferous–Late Permian).

Known geographical distribution: Lodève, Provencal Basins, France; Thüringen, Germany; Sachsen, Dolny Slask, Poland; Russia; western Dolomites, northern Italy; Arizona, Colorado, Indiana, Kansas, Massachusetts, Missouri, New Mexico, Ohio, Pennsylvania, Rhode Island, Texas, West Virginia, Wyoming, USA.

Characters of trackways: quadrupedal; pentadactyl manus and pes; semi-digitigrade impressions; long, slender, curved (towards trackway midline) digits; digit lengths increase I-II-III-IV, V=I (manus), I-II-V-III-IV (pes); manus impressions inturned, pes aligned with trackway midline; secondary coupling; manus trackwitdh narrower than pes trackwidth; stride:footlength up to 4.4:1; footlength 10–80 mm; manus to pes longest digit length ratio 1.0–1.3; pes digit length ratios of 1.5, 1.2, 1.9, 0.5; manus digit length ratios of 1.3, 1.8, 1.9, 0.3.

Previous attributions: *Araeoscelis*, *Kadaliosaurus*, *Petrolacosaurus*, *Paleothyris*, or *Tridentinosaurus* (Haubold 1971*a*); Araeoscelidae (Haubold 1971*b*, 1996, 2000); Araeoscelidae, probably *Petrolacosaurus* or *Araeoscelis* (Haubold and Lucas 2001).

New attributions: Araeoscelididae (= *Araeoscelis* + *Zarcasaurus*) of the Order Araeoscelida (= Araeoscelididae + Petrolacosauridae). The long, gracile limbs and typically 'lacertoid' morphology (very long, slender, curved digits) of araeoscelididan feet suggest a correlation with *Dromopus*. Although there are discrepancies in body size, and the stratigraphical range of *Dromopus* is considerably longer than the known range of the Araeoscelididae, this taxon remains the most likely candidate for the trackmaker of *Dromopus*.

Erpetopus Moodie, 1929 / *Varanopus* Moodie, 1929

Type ichnospecies: Erpetopus willistoni Moodie, 1929; *Varanopus curvidactylus* Moodie, 1929

Other included ichnospecies: V. microdactylus (Pabst, 1896).

Synonymous ichnogenera: The author considers *Erpetopus* and *Varanopus* synonymous, representing two groups of trackways differentiated only by size and not significantly by morphology. However, these two ichnogenera have not as yet been formally synonymised.

***Known stratigraphical range*:** Asselian to Kazanian (Early–Late Permian).

***Known geographical distribution*:** Thüringen, Germany; Colorado, New Mexico, Ohio, Texas, West Virginia, USA.

***Characters of trackways*:** quadrupedal; pentadactyl manus and pes; primary coupling; plantigrade impressions; stride:footlength averages 4:1; digit lengths increase from I-II-III-IV, V=II (manus and pes); straight, slender digits; footlength 5–30 mm; manus and pes inturned towards trackway midline; pes digit length ratios of 2.0, 1.2, 1.3, 0.8; manus digit length ratios of 1.3, 1.5, 1.2, 0.6; manus to pes longest digit length ratio of 1.3.

***Previous attributions*:** Cotylosauria, Captorhinomorpha, Procolophonomorpha or Promillerosauria (Haubold 1971*a*); Procolophonomorpha (Haubold 1971*b*); Captorhinomorpha (Haubold 1998, 2000; Schult 1995); Protorothyrididae, Captorhinidae (Haubold and Lucas 2001).

New attributions: *Erpetopus* / *Varanopus* may represent any of the stem-amniote taxa Procolophonoidae, Varanopsidae, or Captorhinidae. The latter two are the most likely candidates, based upon foot morphology, digit length ratios, and gait patterns.

Hyloidichnus Gilmore, 1927

Type ichnospecies: *Hyloidichnus bifurcatus* Gilmore, 1927.

Other included ichnospecies: *H. major* (Heyler and Lessertisseur, 1963); *Hyloidichnus* sp. Haubold, 1971*a*.

Synonymous ichnogenera: *Gilmoreichnus* Haubold, 1996; *Hylopus* Gilmore, 1927.

***Known stratigraphical range*:** Serpukhovian to Kazanian (Mid-Carboniferous–Late Permian).

Known geographical distribution: Lodève, Provencal Basins, France; Thüringen, Germany; Sachsen, Dolny Slask, Poland; Russia; western Dolomites, northern Italy; Nova Scotia; Shropshire, UK; Alabama, Arizona, Indiana, New Mexico, Ohio, Pennsylvania, Texas, Virginia, USA.

***Characters of trackways*:** quadrupedal; pentadactyl manus and pes; narrow trackway; primary coupling, indicating body length approximately equal to stride length; semi-plantigrade impressions with narrow sole; straight, slender digits; pes stride:footlength ration between 4.1 and 5.1; digit lengths increase from I-II-III-IV, V=I (manus and pes); ratio of manus to pes longest digit length ratio of 0.8; pes digit length ratios of 1.6, 1.3, 1.5, 0.4; manus digit length ratios of 1.5, 1.5, 1.1, 0.3.

***Previous attributions*:** Seymouriamorpha, perhaps *Phanerosaurus*, *Diadectes*, *Diasparactus*, *Discosauriscus*; or *Melanerpeton* (Haubold 1971*a*); *Captorhinus* (Haubold 1971*b*, for Gilmoreichnus); Eothyrididae, a basal synapsid ('pelycosaur') group (Haubold 2000).

New attributions: The most likely candidate taxon is the Procolophonidae, based upon digit length ratios, appropriate body size, proportions, and gait patterns, and similar stratigraphical ranges.

Ichniotherium Pohlig, 1892

Type ichnospecies: *Saurichnites cottae* Pohlig, 1892.

Other included ichnospecies: *I. aequalis* (Heyler and Lessertisseur, 1963); *I. willsi* Haubold and Sarjeant, 1973.

Synonymous ichnogenera: *Saurichnites* Pohlig, 1892; *Sphaerodactylichnium* Pabst, 1895; *Sphaerodactylichnia* Pabst, 1900; *Koryichnium* Nopsca, 1923; *Brontopus* Heyler and Lessertisseur, 1963; *Cyclopus* Heyler and Lessertisseur, 1963.

***Known stratigraphical range*:** Moscovian to Kazanian (Late Carboniferous–Late Permian).

***Known geographical distribution*:** Lodève, Provencal Basins, France; Thüringen, Germany; Sachsen, Dolny Slask, Poland; Russia; Shropshire, UK; Arizona, USA.

***Characters of trackways*:** quadrupedal; manus and pes pentadactyl; large size (up to 140 mm); narrow trackwidth; plantigrade impressions; stride:footlength ratio from 3.5:1 and 5:1; primary coupling; manus and pes inturned towards trackway midline; pes length almost equal to width, with oval, inwards extending heel; manus smaller than pes, but broader; manus to pes longest digit ratios of 1:1; pes digit length ratios of 1.3, 1.3, 1.2, 0.8; manus digit length ratios of 1.3, 1.4, 1.3, 0.7.

***Previous attributions*:** Caseidae (Haubold 1971*a*); *Edaphosaurus* (Haubold 1971*b*); Diadectidae (Haubold 1998); *Diadectes* (Haubold 2000).

New attributions: The Diadectomorpha (Diadectidae + Limnoscelidae) are suggested as the most likely trackmaker candidates for *Ichniotherium*. The author agrees with previous attributions of *Ichniotherium* to diadectid-like forms, however, correlation to genus, or even family level is considered inappropriate, as there are no apomorphies distinguishing members of this taxon. The correlation is based upon digit length ratios, manus and pes proportions, the short, broad phalanges and blunt rounded unguals of this taxon, together with an appropriate stratigraphical range, and suitable body size and proportions.

Conclusions

1. The combination of trackway and body fossil data is better achieved when ichnological classifications are based upon the morphological features of trackways that relate directly to trackmaker anatomy and not to sedimentary or ethological influences.
2. Trackways cannot be attributed to biotaxa with any degree of certainty without the use of character-based methods, in conjunction with phenetic and coincidence correlation techniques.
3. The identified groups of likely trackmaker candidates for common Late Palaeozoic ichnotaxa are predominantly familial, or of higher rank (such as in the case of the attribution of

Ichniotherium to the class Diadectomorpha). In addition, only in a few cases can an ichnogenus be unequivocally assigned to any single monophyletic group, and generic assignations as specified by many authors are highly speculative. This highlights the fact that even under a purely morphological, numerical trackway classification, ichnotaxa do not mirror biotaxa (Farlow and Pianka 2000), and an ichnological classification does not provide any insight into evolutionary relationships without combining the data with synapomorphy-based, phylogenetic analyses. Nevertheless, the method described above is the optimal approach given all available data. Identification to family, or perhaps class level is possible, and this can still be useful in palaeoecological and biomechanical studies.

CHAPTER 5

TAXON DISPLACEMENT AND ADAPTIVE RADIATION IN TERRESTRIAL TETRAPOD COMMUNITIES OF THE LATE PALAEOZOIC: A NEW PERSPECTIVE

Introduction

The Late Carboniferous and Permian represent a key stage in the evolution of tetrapod faunas. The stem-lissamphibian ('temnospondyl') assemblages of the Carboniferous declined with the appearance of the amniotes during the later stages of this period, producing a transition to predominantly terrestrial communities that continued into the Permian. This apparent faunal turnover represents one of the largest such events in vertebrate evolutionary history. Although the first land vertebrates only appeared during the Late Devonian (Coates 1996; Clack 1997, 2002*a*), by the Early Permian amniotes had become the dominant terrestrial forms, and had diverged to form three major clades: the Synapsida (stem-mammals), Diapsida (reptiles and birds), and Testudines, or turtles (Laurin and Reisz 1995).

A number of models have been formulated to explain the patterns of faunal turnover observed during this Late Palaeozoic transition. These models invoke a variety of intrinsic and extrinsic influences on early tetrapod evolution. Benton (1979, 1996*a*, *b*) systematically examined two of these models, namely, competitive taxon displacement and adaptive radiation, both concerned with intrinsic evolutionary effects. Benton (1979) concluded that early tetrapods evolved in stages, each stage representing the radiation of a new group into a new habitat or set of niches. He recognised three large-scale stages of tetrapod expansion: the first was of amphibious stem-tetrapods into aquatic and semi-aquatic niches; the second of amniotes into warm, fully terrestrial conditions; and the third of mammals into colder habitats and nocturnal activity patterns. Following a detailed examination of the likelihood of competition between individual families of tetrapods throughout the Late Palaeozoic, Benton (1996*a*, *b*) concluded that the role of direct competition in promoting this displacement was relatively small, and that faunal turnover within early tetrapods was driven by adaptive radiation. However, the effects of direct competition between groups of early tetrapods, ultimately leading to extinction or significant decline in stem-lissamphibian diversity and abundance, cannot be totally discounted.

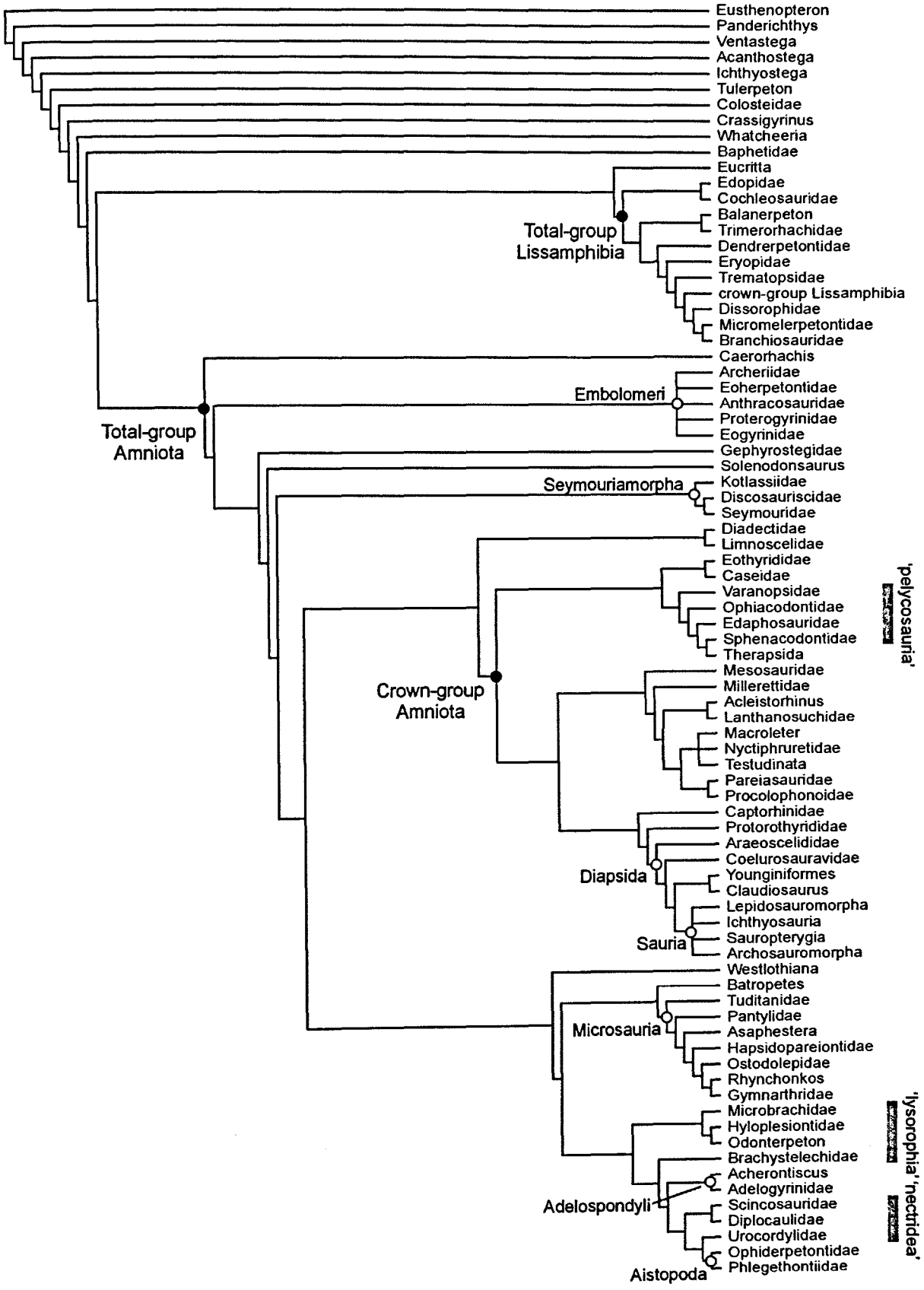
An intrinsic change in temnospondyl habitats forms the basis for the third model. Carroll (1988) noted that temnospondyls of the Late Carboniferous and Early Permian were primarily terrestrial, whilst those of the Late Permian and Triassic became increasingly aquatic. The possibility of stem-lissamphibians being forced to retreat to aquatic habitats by the dominance of amniotes within the terrestrial environment is considered here. Although this model involves competitive interaction between stem-lissamphibians and amniotes, it differs from the competitive taxon displacement model

by suggesting that temnospondyls were not driven to extinction or large-scale decline by amniote dominance, but merely responded by moving to new habitats.

Lastly, the fourth and final model to be evaluated involves an extrinsic influence. The effects of Late Palaeozoic climate change upon early terrestrial tetrapod communities is not fully understood, although a number of authors have examined adaptations in amniotes to dry, terrestrial environments (e.g. Romer 1957, 1967; Reisz 1986; Carroll 1988; Frolich 1997; Graham *et al.* 1997; Clack 2002*a*). These adaptations are not possessed by stem-lissamphibians, and so climate change may potentially have played a significant role in their decline.

This study charts the development of terrestrial tetrapod communities across this Late Palaeozoic faunal transition with the use of both new and revised data from trackway localities across present day North America and Europe. This is a novel method, which aims to use a synthesis of trackway data, in conjunction with body fossil data, in order to review and test the four suggested models of Late Palaeozoic tetrapod faunal turnover from a new perspective. Tetrapod community development is considered using estimates of the relative proportion of individuals of the clades Lissamphibia (concentrating upon stem-lissamphibian 'temnospondyls'; Ruta *et al.* 2003) and total-group Amniota (Fig. 5.1) within Permo-Carboniferous trackway assemblages. Within trackways, the characteristic number of digits on the manus distinguishes lissamphibians and amniotes (Chapter 4). A tetradactyl manus (with pentadactyl pes) is a synapomorphy of lissamphibians, whilst terrestrial amniotes exhibit five digits on both the manus and pes. Although stem-amniote microsaurs also exhibit a tetradactyl manus, these are small forms and can be discounted as the potential trackmakers of larger trackways (Chapter 4). The present state of trackmaker-trackway correlation (Schult 1995*a*; Carrano and Wilson 2001) is such that trackmakers cannot be further identified with a high degree of accuracy, although this is not necessary for this study.

Whilst it is widely known that trackway assemblages can provide population data not yielded by body fossils, this is the first study to extend this knowledge to provide insight into patterns of faunal turnover, adaptive radiation, and taxon displacement. However, a number of studies based upon vertebrate and invertebrate *skeletal* material have focused upon faunal turnover, particularly in terms of competitive radiation and adaptive expansion (e.g. Benton 1979, 1996*a*, *b* (tetrapods); Gould and Calloway 1980 (brachiopods and bivalves); Charig 1984 (therapsids and archosaurs); Krause 1986 (rodents and multituberculate mammals); Lidgard *et al.* 1993 (bryozoans); Sepkoski 1996 (bivalves and brachiopods); Maas *et al.* 1988 (plesiadapiform mammals); Purnell 2001 (agnathans and gnathostomes)). However, these studies relied mainly upon estimates of taxon abundance illustrated by taxonomic richness diagrams. These estimates, although they do give some indication of familial diversity at certain times in the geological record, do not provide a measure of absolute numbers of



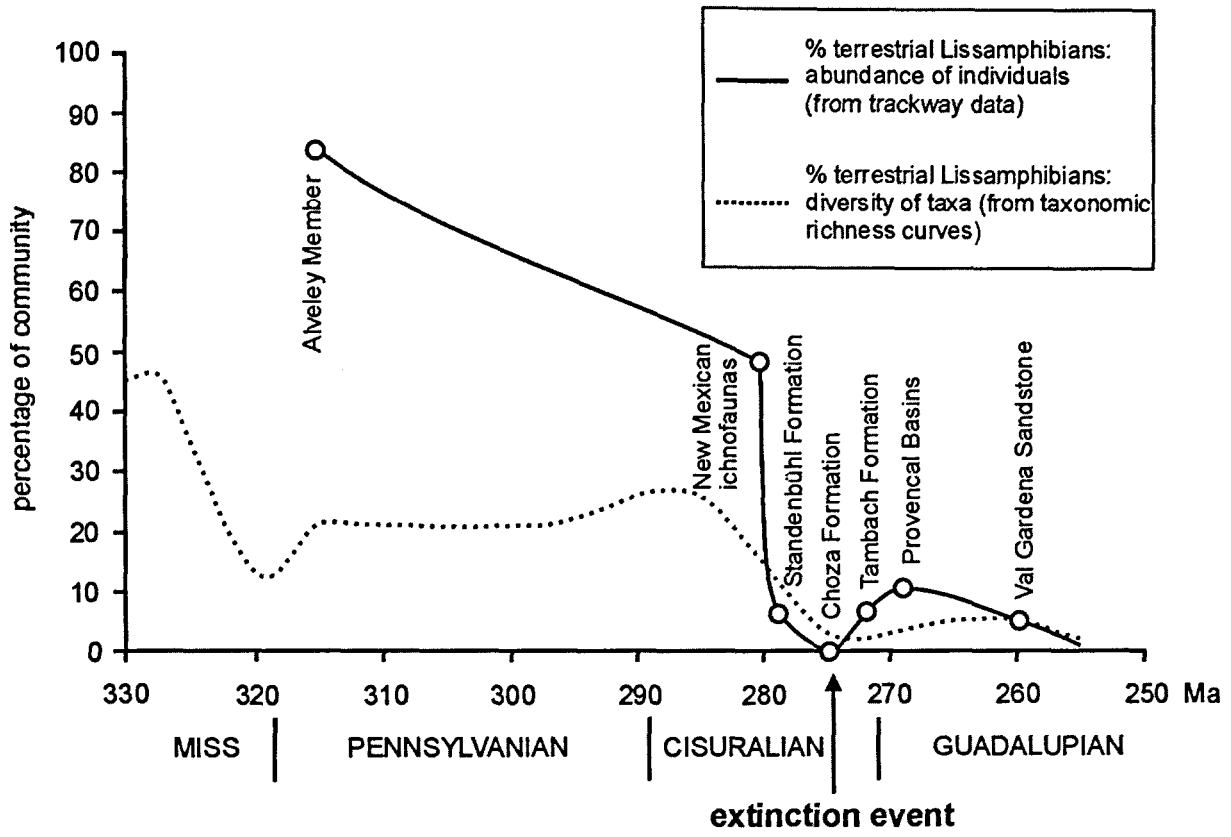
TEXT-FIG. 5.1. Early vertebrate phylogeny illustrating relationships between Lissamphibia and Amniota, and the taxa within these clades. Data from the combined phylogenies of Reisz (1986); Laurin (1993); Gauthier (1994); Laurin and Reisz (1995); Lee (1995); Ruta *et al.* (2003).

individuals. Benton (1979) considered that this is impossible to calculate within palaeofaunas, but trackway assemblages can provide a semi-quantitative estimate of abundances of individuals (Cohen *et al.* 1993; see 'Biases and artefacts', below), and these data may give considerably different assessments of populations (Fig. 5.2). Therefore, whilst it may be estimated from taxonomic richness diagrams that relative abundances of taxa changed through time – dependent upon the recorded number of families, for example – using trackways enables a determination of whether the proportion of these taxa within a community changed in terms of an estimate of the numbers of individuals. This is important, because a taxon may go into decline in terms of absolute numbers of individuals, but this may not be evident from taxonomic richness diagrams if the taxon does not go completely extinct. The use of trackway data in conjunction with body fossil data thereby has the potential to greatly increase the understanding of terrestrial community dynamics and taxon interactions.

Biases and artefacts: the body fossil record

Palaeocommunity composition is typically assessed using body fossil accumulations. The relative number of individuals of certain taxa within vertebrate palaeocommunities can be evaluated using an estimate of the Minimum Number of Individuals (MNI). Within each sample, the MNI is determined by counting the single most common element present within the assemblage (e.g. left femur, right distal humerus; e.g. Behrensmeyer 1991). However, the accuracy of the MNI estimate depends strongly on the level of disarticulation and fragmentation of the skeletal material, and the degree to which this causes incorrect identifications of taxa within the assemblage. Estimates of the relative abundance of species or individuals within the sample may therefore become inaccurate (Brett 1990).

In addition, a number of facies-based and taphonomic biases act in concert to potentially alter the life associations of vertebrate groups, in terms of individual species and groups of taxa, before preservation in the fossil record. These biases must also be considered before a realistic determination of the MNI or relative taxon abundances within a skeletal assemblage can be made. A frequent bias in fossil vertebrate accumulations results from the transportation of skeletal material after death (Behrensmeyer 1990, 1991). Movement often occurs away from the original habitat, to a site more favourable for burial, giving long-term, time-averaged attritional samples composed of spatially and temporally mixed associations of taxa, rather than a true representation of original community structure (Jablonski *et al.* 1986). The differential transportation of various bones – by water, or predator activity, for example – also results in taxa appearing absent from the life association (Behrensmeyer 1990, 1991). Repeated burial and reworking of skeletal material can contribute to this bias, producing further time-averaging within samples (Behrensmeyer 1990). Other biases include the differential effects of taphonomy (soft-bodied organisms are rarely preserved, for instance), and the chemical alteration of skeletal elements (Behrensmeyer 1991).



TEXT-FIG. 5.2. Percentage of stem-lissamphibians in terrestrial tetrapod communities of the Carboniferous and Permian. Solid line represents percentages based upon abundance of individuals, taken from trackway data (Fig. 5.4). Dotted line represents percentages based upon estimates of lissamphibian abundance derived from number of families per stratigraphic stage (taxonomic richness diagrams; Fig. 5.3). Miss: Mississippian. Absolute dates from Menning *et al.* (2000, 2001), Remane *et al.* (2000), and Wardlaw and Davydov (in press).

Biases and artefacts: the trace fossil record

Many problems associated with bias in the body fossil record do not apply to trace fossils (for example, the effects of disarticulation, transportation, reworking, and the differential influences of these factors). In addition, soft-bodied taxa, as well as those with a hard skeleton, may be represented. Nevertheless, biases and artefacts are apparent when using trackway data to interpret palaeocommunity structure. For example, the relative differences in trackmaker activity levels are difficult to account for, so that more active taxa may be over-represented. Furthermore, the trackway record tends to preserve more traces of depositional environment generalists than those of habitat specific groups (Cohen *et al.* 1993), and smaller taxa are less likely to be represented than larger ones (Cohen *et al.* 1993; Farlow and Pianka 2000). As the depositional environments favouring trackway preservation are limited in terrestrial environments, not all aspects of a terrestrial palaeocommunity can be covered, and time-averaging remains a potential biasing factor unless all trackways under consideration originate from a single bedding plane, or rapidly deposited geological horizon.

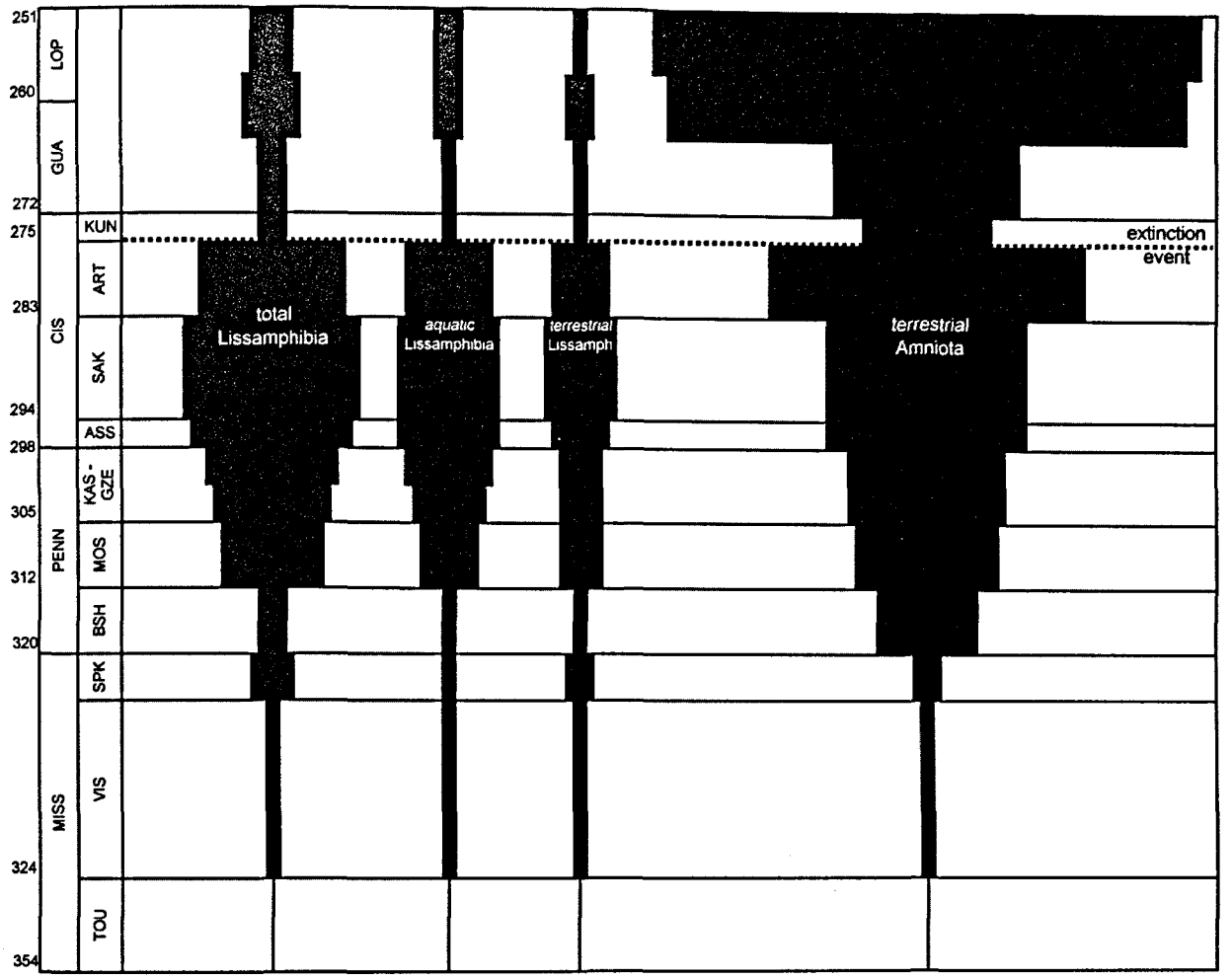
Cohen *et al.* (1993) demonstrated, through the study of modern mammal communities within marginal lacustrine and fluvial environments, that trackways can be an effective indicator of biodiversity. Over 96 per cent of biotaxa recorded at their census site were represented by trackways within the same area. In terms of the taxon abundances within the community, Cohen *et al.* (1993) and Farlow and Pianka (2000) concluded that trackways cannot be used as a very accurate indicator of the relative numbers of individuals within certain species, although Cohen *et al.* (1993) found that if the mean activity levels and stride lengths of these species were taken into account, better results were obtained. However, at a higher taxonomic level / lower resolution (e.g. Carnivora vs. Artiodactyla), Cohen *et al.*'s trackway data did reflect the relative abundances of biotaxa within the community: the Artiodactyla accounted for 99.7 per cent of total standing diversity, and 94.9 per cent of trackways; Carnivora accounted for the remainder. Cohen *et al.*'s (1993) study in itself already incorporates bias, as taxon diversity counts were made only during daylight hours, thereby under-estimating the true abundance of nocturnal carnivore species. Once this bias is accounted for, the study demonstrates that trackways can be used as a semi-quantitative proxy for relative abundances of individuals at high taxonomic levels within a community. Trackway data may therefore enable estimates of, for example: community structure (in terms of taxa present) and the relative proportions of different groups within the community; abundance of individuals of a single taxon; the preferred habitats, or ecological niches, of certain taxa; the range of body sizes both within populations and single taxa; and possible taxon interactions, such as predation (e.g. Lockley and Madsen 1993; Kramer *et al.* 1995).

Using high-level clades, such as Amniota and Lissamphibia, in evolutionary and community development studies inevitably leads to some loss of resolution. However, due to the nature of the fossil record – often incomplete – and the low time resolution of the terrestrial stratigraphical record,

tracing evolutionary processes at species level can be inaccurate. Using higher-level clades presents an alternative method, which is nevertheless very informative. As trackways cannot, in most cases, be identified to generic or sometimes even familial level (Chapter 4), the interactions and development of lower vertebrate taxa cannot be studied through the use of trace fossils. However, although the evolutionary development of different families of certain groups may be influenced by different factors (Benton 1979; Maas *et al.* 1998), those taxa that occupy the same habitats, are of similar morphology, and rely upon the same food sources are, in principle, exposed to the same environmental and ecological pressures, and constrained by the same limitations, as they generally occupy the same adaptive zones. It must be remembered, however, that the adaptive zone of a generic or species-level taxon may change during ontogeny – particularly within stem-lissamphibians, since many semi-terrestrial representatives have an aquatic larval stage – and so this disparity must be considered. Trackways do not take these changes in habitat through ontogeny into account, nor can they be implemented in the study of aquatic clades. In addition, the range of environments within which terrestrial communities can be examined is somewhat limited, as trackway preservation is favoured only by certain conditions, so the study of community development through time is restricted to certain habitats. However, this is not a large problem, as a study of community development is only valid if palaeofaunal data are taken from taphonomically comparable deposits representing similar environmental settings (Jablonski *et al.* 1986).

The end-Artinskian extinction event as an extrinsic influence on early tetrapod evolution

The end-Artinskian extinction event is crucial to understanding the relative effects of intrinsic and extrinsic factors in influencing Late Palaeozoic tetrapod faunal turnover. This event was first identified by Benton (1989*a*, *b*), who inferred the loss of 15 families of early tetrapods, including members of both the Lissamphibia and Amniota. This loss was considered to constitute 58 per cent of total pre-event familial diversity, although it was mainly amniotes that were affected (Benton 1989*a*). Seven families of actinopterygians were also lost (Gardiner 1993). The fossil record of the Permian is considered by some authors (e.g. Benton 1989*a*) to be more than 75 per cent complete, and so it is unlikely that the end-Artinskian event is an artefact. However, the evidence for this extinction event within other vertebrate groups is less conclusive. Although Aldridge (1988) recognised high extinction rates within the Conodonta during the Early Permian, this appears to have resulted from a gradual, stepwise diversity reduction in a low diversity assemblage, with a maximum of six species lost at the Artinskian–Kungurian boundary (Sweet 1988). Seven families of palaeonisciform chondrostean fish were lost during the Sakmarian, but only one family was lost during the Artinskian (Benton 1989*a*). Among the major groups of marine invertebrates, faunal turnover across the Artinskian–Kungurian boundary has been recorded – for example, within the reef communities described by Kossovaya *et al.* (2001) and Weidlich (2002) – but this appears to result from sequence stratigraphic change rather than



TEXT-FIG. 5.3. Newly compiled taxonomic richness diagrams for the stem-Lissamphibia (terrestrial, aquatic, and combined) and total-group Amniota during the Late Palaeozoic. Width of bar proportional to number of families recorded per stage. Monospecific families not recorded (except for first occurrences of Lissamphibia and Amniota in the Viséan). Based upon the phylogenetic analyses of Reisz (1986); Laurin (1993); Gauthier (1994); Laurin and Reisz (1995); Lee (1995); Ruta *et al.* (2003) and Late Palaeozoic tetrapod family census taken from the literature (Carroll 1988; Benton 1993; Milner 1994; Milner and Sequeira 1994, 1998; Clack 1994, 1998, 2001, 2002*b*; Lombard and Bolt 1995, 1999; Coates 1996). Art: Artinskian; Ass: Asselian; Bsh: Bashkirian; Cis: Cisuralian; Gua: Guadalupian; Gze: Gzelian; Kas: Kasimovian; Kun: Kungurian; Lop: Lopingian; Miss: Mississippian; Mos: Moscovian; Penn: Pennsylvanian; Sak: Sakmarian; Spk: Serpukhovian; Tou: Tournasian; Vis: Viséan. Absolute dates and stage names from Menning *et al.* (2000, 2001), Remane *et al.* (2000), and Wardlaw and Davydov (in press).

extinction, and is therefore subject to facies biases. Neither is there any evidence for extinction within one of the major rock-forming groups, the Foraminifera (Hart and Williams 1993). It is pertinent to note, therefore, that although the tetrapod fossil record appears to clearly demonstrate a substantial reduction in familial diversity (Fig. 5.3), this event has not been subject to rigorous analysis for artefacts of the kind noted by Smith (2001).

Trackway localities: background, fauna, sedimentary environments

The Late Palaeozoic vertebrate trackway record is characterised essentially by two types of ichno-assemblage: 'fluvial-alluvial', and 'sand-dune' associations. The majority of European and North American vertebrate ichno-assemblages are found within red-beds deposited in fluvial floodplain and alluvial fan settings. These trackway localities display a cosmopolitan ichnofauna throughout the Permian, predominantly comprising the ichnogenera *Limnopus (Batrachichnus)* Woodworth, 1900; *Limnopus* (*Limnopus)* Marsh, 1894; *Amphisauropus* Haubold, 1970: *Dimetropus* Romer and Price, 1940; *Dromopus* Marsh, 1894; *Hyloidichnus* Gilmore, 1927; and *Ichniotherium* Pohlig, 1885 (Haubold 1970, 1971*a*, *b*, 1973, 1998, 2000; Haubold and Katzung 1975; Conti *et al.* 1977; Holub and Kozur 1981; Fichter 1983*a*, *b*, 1994; Gand 1985; Boy and Fichter 1988; Demathieu *et al.* 1992; Hunt *et al.* 1995*a*, *b*; Lucas and Heckert 1995; Haubold and Stapf 1998; Hunt and Lucas 1998; Tucker and Smith in press). However, 'sand-dune' associations are less frequent, and exhibit low diversity ichnofaunas consisting predominantly of *Chelichnus* Jardine, 1850, with occasional trackways of *Dromopus* (Lull 1918; Gilmore 1926, 1927, 1928; Baird 1952; Schmidt 1959; Haubold 1971*a*; Brand and Tang 1991; McKeever 1991, 1994; Fichter 1994; Morales and Haubold 1995; Haubold *et al.* 1995; Lockley *et al.* 1995; McKeever and Haubold 1996; Hunt and Lucas 1998). Morphologically, *Chelichnus* as an ichnogenus is highly controlled by sedimentary facies; trackmaker anatomy plays only a minor role in comparison. Therefore, as 'sand-dune' ichno-assemblages represent facies-controlled ichnofaunas, and show no significant change through time or localised space, this study concentrates upon fluvial/alluvial associations that represent the majority of Late Palaeozoic trackway assemblages. It must be remembered, nevertheless, that the precise depositional environment of these trackway faunas affects the abundance and diversity of the component ichnotaxa. This must be considered when examining patterns within and across Late Palaeozoic ichno-assemblages.

The vertebrate trackway localities considered here have been specifically chosen for a number of reasons; certainly, the list of selected sites is not exhaustive. Firstly, these localities represent the major Late Palaeozoic ichno-assemblages across Europe and North America, representing Laurasian faunal associations; those of Gondwana are not considered here. Trackway collections that the authors have seen were chosen preferentially, and the choice of other localities was largely constrained by the amount of information available in the literature. Importantly, the selected trackway collections

represent vertebrate traces from similar depositional environments to as great a degree as possible, as the analysis of the development of communities from a number of vastly different environmental settings would merely lead to inaccurate, artificial conclusions. In order to fully appreciate the context of individual trackway sites, it is critical to have an understanding of the related depositional environments; a brief summary of these is therefore given below.

Alveley Member, Salop Formation, Shropshire, UK

Vertebrate trackways from the Alveley Member of the Salop Formation (Warwickshire Group) were discovered by Dr F. Raw in 1914. Haubold and Sarjeant (1973, 1974) undertook a preliminary study of the material, based upon the best-preserved trackways, but Tucker and Smith (in press) provide the first comprehensive appraisal. The presence of invertebrate trackways (*Koupichnium* Nopsca, 1923) and plant fossils (e.g. Lycopsida, Sphenopsida) is indicative of alluvial and shallow lacustrine palaeoenvironments. The Alveley Member contains 152–247 m of Westphalian D (Moscovian) sediments (Besly and Cleal 1997; Johnson *et al.* 1997; Powell *et al.* 2000), described as those of an alluvial floodplain (Whitehead and Pocock 1947; Glover and Powell 1996; Besly and Cleal 1997). The bulk of the succession comprises interbedded red mudstones and red to red-brown, fine- and medium-grained sublitharenitic sandstones, interspersed with thin, white and black *Spirorbis* limestone horizons, in association with clay bands comprising illite and kaolinite (Besly and Cleal 1997). The presence of minor caliche palaeosols is indicative of semi-arid climatic conditions. The succession at the trackway locality consists of red mudstone and clay horizons alternating with fine- to medium-grained, red and grey, sheet and channel sandstones. Vertebrate trackways occur as positive casts upon the bases of these sandstone beds, together with raindrop imprints, desiccation cracks and fluted tool marks, indicative of a periodic emergence of the underlying mudstone and clay horizons.

Earp Formation, Big Hatchet Mountains, Hidalgo County, New Mexico

A variety of both marine and non-marine fossils have been found within the Earp Formation in south-western New Mexico (Hidalgo Co.), including freshwater and marine invertebrates, fish scales, conifer impressions and tetrapod footprints. Baird first identified tetrapod trackways of the Earp Formation, as reported by Zeller (1965), whilst Lucas and Hunt (1995) published a more extensive review. The formation represents deposition upon a supratidal flat with little marine influence (Cook *et al.* 1998; Lucas and Hunt 1995). This interpretation contrasts with that of the type section, in Arizona, USA, which consists of intercalated marine and non-marine units, interfingering at the base with limestones of the underlying Horquilla Formation. In comparison, the section in the Big Hatchet Mountains rests unconformably upon the Horquilla limestones. A basal conglomerate comprising rounded Horquilla clasts within a red, ferruginous, micritic matrix fines upwards into a sequence of intercalated siliciclastic and carbonate strata, dominated by reddish calcareous mudstones with minor yellow siltstones. These mudstones include root casts and pedogenic nodules indicative of emergent and soil

horizons, whilst the siltstones exhibit ripple lamination. In the upper part of the section, the Earp Formation interfingers with the overlying Colina Limestones. Thickness varies from 826 to 270 m (Cook *et al.* 1998), thinning south-westwards into Arizona and Mexico.

Robledo Mountains Member, Hueco Formation, Dona Ana County, New Mexico

The Hueco Formation consists of four laterally persistent members, the third youngest of which, the Robledo Mountains Member, includes large numbers of tetrapod trackways within a single stratigraphical horizon covering an area of approximately 20 km^2 (Lucas *et al.* 1995*b*). Vertebrate trackways from the Hueco Formation were first documented by LeMone *et al.* in 1971, as recorded by Lucas *et al.* (1995*a*). Subsequent mention of these was made in the literature (e.g. MacDonald 1992, 1994), but the most comprehensive accounts can be found in numerous contributions by Hunt, Lucas, and associates (e.g. Lucas 1993; Hunt *et al.* 1993, 1994 *a*, *b*, 1995*d*; Lucas *et al.* 1994, 1998; Lucas and Heckert 1995; Haubold *et al.* 1995; Schult 1995*a*, *b*). The Robledo Mountains Member, previously known as the Abo Formation, Abo-Hueco Member, or Abo Tongue (Lucas *et al.* 1995*b*; Cook *et al.* 1998; Lucas *et al.* 1998) is over 125 m thick at the type section, consisting predominantly of carbonate strata typical of the Hueco Formation. These were deposited in fairly shallow water, low energy, marine conditions, and show a change upwards through the member from sedimentation in perhaps brackish environments with restricted water circulation, to deposition within an open marine shelf (Lucas *et al.* 1995*b*). Interbedded with the carbonate horizons are siliciclastic red-beds deposited within a tidal flat environment. The intercalating limestones and shales are predominantly micritic, although bioclastic wacke- and packstones do occur in association with calcareous shales. Faunal elements include marine invertebrate megafossils, dominated by bryozoans and brachiopods, with less frequent molluscan forms, and a wide variety of foraminiferans and ostracods. Conodonts from marine strata interbedded with red-bed horizons give the Robledo Mountains Member an age of Early Artinskian (Early Permian; Lucas *et al.* 1995*b*). Vertebrate tracks occur within the intertidal, mixed sand- and mud-flat red-beds. These comprise fine-grained, micaceous, litharenitic sandstones, with minor mudstones and siltstones. Sedimentary structures include ripple and planar laminations, and rare trough, hummocky and herring-bone cross beds. Rain prints, leaf impressions, and desiccation cracks are also found in association with the tetrapod trackways (Lucas *et al.* 1995*b*; Cook *et al.* 1998).

Abo Formation, Socorro County, New Mexico

Vertebrate tracksites from the Abo Formation were documented by Hunt *et al.* (1990, 1995*c*), and Lucas *et al.* (1995*b*). In east-central and south-eastern New Mexico, the Abo Formation lies conformably above the Bursum Formation, which consists of intercalated siliciclastic and carbonate horizons with both vertebrate and invertebrate body fossils, and invertebrate tracks. Vertebrate trackways are not found in the Bursum Formation, but appear in three main areas of Abo outcrop in Socorro County: near Bingham; at the Abo Pass; and east of the Rio Grande, across from Escondida

(Hunt *et al.* 1995*c*). The top of the Abo Formation in Socorro County grades conformably into the Meseta Blanca Member of the Yeso Formation, a tabular bedded sandstone member with salt casts and a few poorly preserved vertebrate trackways. Hatchell *et al.* (1982) recognised two units within the Abo Formation: a lower arkose, conglomerate and mudstone (ACM) unit, and an upper rhythmically bedded sandstone and mudstone unit. The ACM represents low energy deposition within low sinuosity channels, upon an alluvial floodplain with small, shallow ephemeral lakes and broad channels, whilst the upper strata include evidence of small, high sinuosity, muddy channels with occasional calcretes, desiccation cracks and *Walchia* conifers, indicative of a periodically dry climate (Mack *et al.* 1995). Towards northern New Mexico, the Abo Formation represents inland fluvial facies, whereas upper supratidal flats are represented in the south (Lucas *et al.* 2001). Track-bearing horizons, found mostly within the lower third of the Abo Formation within the upper half of the ACM unit (Hunt *et al.* 1995*c*) are characterised by tabular, medium to coarse-grained sandstones. The trackways are usually found upon upper bed surfaces, in association with clay drapes, rare invertebrate tracks, infrequent seed ferns, and *Walchia* conifers.

Sangre de Cristo Formation, Sangre de Cristo Mountains, San Miguel County, New Mexico

Hunt *et al.* (1990) were the first to record tetrapod tracks from the Sangre de Cristo Formation, which were subsequently reviewed by Hunt *et al.* (1995*a*, *b*) and Hunt and Lucas (1998). The Sangre de Cristo Formation in San Miguel County crops out along the southern and eastern margins of the Sangre de Cristo Mountains, and in most places overlies Precambrian basement rocks unconformably. Thickness increases northwards, from 150 m near Pecos in north-central New Mexico, to 2875 m to the north of the New Mexico-Colorado border. Dominant lithological units of the Sangre de Cristo Formation include coarse arkosic sandstones and conglomerates, red and green-grey mudstones and siltstones, and infrequent muddy limestones, with occasional carbonaceous shale and impure coal horizons in the lower part of the section. Two megasequences are recognised (Cook *et al.* 1998), the lower representing an aggrading, braided alluvial fan, characterised by vertically stacked, tabular conglomerates, and an upper megasequence of upward-fining, interbedded sandstones and conglomerates with minor lacustrine limestones, representing a retrograding alluvial fan associated with the diminishing Cimarron arch sediment source. Overall, the Sangre de Cristo Formation typifies a southward thinning wedge of braided alluvial and lacustrine sediments, with southward palaeocurrents.

Choza Formation, Castle Peak, Taylor County, Texas

Documentation of tetrapod trackways in the Choza Formation began when Moodie (1929, 1930) erected the ichnogenera *Erpetopus*, *Microsauropus*, *Varanopus*, and *Solidopus* from the Castle Peak Locality. Sarjeant (1971) erected another ichnogenus, *Moodieichnus*, from the assemblage. However, following a review of all Permian ichnotaxa, Haubold (1971*a*) subsequently proposed a taxonomic

revision of these ichnotaxa and reduced the number of ichnogenera in the Choza Formation to the three accepted at present (*Erpetopus*, *Dromopus*, *Varanopus*). Haubold and Lucas (2001) provided a review of the Choza Formation trackways, suggesting that this low number of ichnogenera may be due to facies-selective factors. The formation, which constitutes part of the upper Clear Fork Group, was deposited on the eastern shelf of the marine, Permian Midland Basin, and comprises intercalations of fluvial and lacustrine red-beds with thinly-bedded marine dolomites. The single vertebrate track-bearing horizon, occurring within a red-bed sequence, is 20 cm thick and consists of ripple-laminated calcareous siltstones. The trackway-bearing part of this horizon is laterally traceable across 1000 m^2 around the northern foot of Castle Peak. This stratum is interpreted as a lacustrine or playa siltstone within an alluvial floodplain environment that was subject to periodical, local marine incursions (Haubold and Lucas 2001).

Tambach Formation, Thüringen, central Germany

Extensive vertebrate remains and trace fossils derive from Bromacker, 1.5 km north of Tambach-Dietharz in Thüringen, Germany (Haubold 1998; Eberth *et al.* 2000; Voigt and Haubold 2000; Voigt 2001). Vertebrate traces are found within the Tambach Formation at a single, stratigraphically clear tracksite (Haubold 1998), which preserves an advanced ichnofaunal assemblage of inferred amniotes, represented by four distinct ichnotaxa. These trackways were first discovered in the Tambach Basin by H. F. Schäfer in 1887, as documented by Scheibe (1890). A preliminary description was made by Pohlig (1885), and extended studies were undertaken between 1895 and 1908 by Pabst (1895, 1897, 1900, 1905, 1908). Later studies include those of Korn (1933), Müller (1954), Haubold (1971*b*), Fichter (1998), and Voigt (2001). Associated body fossils are also found at the Bromacker locality (Sumida *et al.* 1996; Eberth *et al.* 2000), representing an advanced, terrestrial upland community, composed predominantly of diadectids, with a noticeable absence of aquatic and semi-aquatic forms and larger carnivorous synapsid species. A low diversity of invertebrate trackways (*Tambia spiralis*), and the typically upland floral (seed fern and conifer) imprint assemblages reflect the restricted environment within a small, internally drained basin (Eberth *et al.* 2000). Consequently, the diversity of ichnotaxa is low in comparison with other European localities. This is likely to be a reflection of the confined habitat in which these animals were purported to live. In addition, the absence of amphibious forms and their trackways is indicative of a relatively low stability environment within an upland setting. Eberth *et al.* (2000) provide a comprehensive evaluation of skeletal fossils from Bromacker, together with a detailed palaeoenvironmental analysis. Stratigraphically, the Tambach Formation represents the basal 200–400 m of Upper Rotliegend sediments in the Thüringer Wald area, comprising a thick succession of conglomerates, sandstones and mudstones. Deposition occurred within the Tambach Basin, a small graben less than 250 km^2, connected during the sedimentation of the Upper Rotliegend to the larger, NE–SW-trending, Variscan Saale Basin. Footprint beds occur as stacked, fining-upwards sandstone sheets, tens of metres thick (Eberth *et al.* 2000). Horizontal

lamination and low angle cross-stratification are present, and trough cross-bedding indicates a north to north-east palaeoflow.

Standenbühl Formation, Saar-Nahe Basin, south-western Germany

Tetrapod and arthropod trackways from the Upper Rotliegend of southwestern Germany were first identified by Schmidtgen (1927), at Nierstein. Further Permian trackway discoveries were made in 1955 by Reineck, at Martinsheim and Sobernheim, and in the Standenbühl Formation at Nierstein from 1974 onwards, as documented by Fichter (1983*a*, *b*, *c*, 1984), Boy and Fichter (1988), and Haubold and Stapf (1998). Forty-three separate localities within the Saar-Nahe Basin bear vertebrate trackways; these all occur within the Nahe Group (Fichter 1983*b*). This sequence mainly comprises typical Upper Rotliegend alluvial fan and playa sediments of the Wadern, Kreuznach and Standenbühl Formations, including the Nierstein Formation in the Nierstein Horst area (Fichter 1983*b*; Haubold and Stapf 1998). The trackway data considered here, however, originate from the Standenbühl Formation only. This formation comprises predominantly red siltstones in which trackway preservation can be strongly sedimentologically controlled (Haubold and Stapf 1998); care is therefore required in trackway analysis as undertracks are particularly frequent. Sedimentary structures such as raindrop imprints and desiccation cracks indicate periodical emergence and drying of the trackway horizons, and the main lithofacies are interpreted as fluvio-lacustrine, lacustrine and playa. This sequence contrasts with the underlying, fine-grained Lower Rotliegend sediments, which were deposited in a sub-aquatic environment, as indicated by the grey colouration and presence of the arthropod trackway *Isopodichnus* (Fichter 1983*b*).

Provencal Basins, southern France

Numerous vertebrate tracks, invertebrate traces (including *Dendroidichnites*, *Gordia* and *Planolites*), plant fragments and invertebrate body fossils are found within the Provencal Basins of southern France, along a transect between Toulon and Cannes on the Mediterranean coast (Demathieu *et al.* 1992). These have been described by Gand (1980, 1988), Heyler and Montenat (1980) and Toutin (1980). Demathieu *et al.* (1992) provided a comprehensive revision and comparison of the faunas from the different basins, concluding that the assemblages are all very similar. Differences can be noticed, however, in the local distribution of some ichnotaxa. For example, *Limnopus* (*Batrachichnus*) is found predominantly at lake margins, whilst larger forms such as *Limnopus* (*Limnopus*) and *Dimetropus* are more common both within slightly more upland areas within the floodplain environments, and along the edges of the aquatic zones, where it is postulated the trackmakers found a source of food (Demathieu *et al.* 1992). Stratigraphically, these Upper Permian ichnofaunas occur within a succession consisting of four formations (Pradineaux, Mitan, Muy, Motte), all of which represent fluvial floodplain sediments (Demathieu *et al.* 1992). These are typically argillaceous, and associated with muddy lacustrine sediments, carbonates, paludal sediments with calcareous nodules, and Late Permian

tuffs. Vertebrate trackways occur as convex hyporeliefs within the finest grained deposits, and are associated with raindrop prints and desiccation cracks, indicating alternate wet and dry periods; Demathieu *et al.* (1992) hypothesised that this is congruent with a seasonal Late Permian climate.

Val Gardena Sandstone, western Dolomites, northern Italy

Conti *et al.* (1977) provided a comprehensive review of vertebrate footprints found in the Val Gardena Sandstone. These studies followed the work of Leonardi from 1951–1960, and are based upon two seasons of field collection by the authors. It should be noted that the footprints do not originate from a single horizon, and so cannot give direct information about distinct, isolated, communities. However, the large amount of material recorded (340 specimens) should provide a fairly accurate representation of population compositions during the Late Permian. The trackways considered here originate from the same sedimentary environment and have been subject to a taxonomic review – as comprehensive as Conti *et al.*'s (1977) descriptions and figures allow – by the present author for the purposes of this study. The Permian Val Gardena Sandstone represents the first clastic sedimentary formation in the southern Alps following the Late Carboniferous Variscan orogeny. It directly overlies the quartz porphyry basement, except in the Carnico-Bellunese Basin of north-eastern Italy, where it overlies marine sediments of the Permo-Carboniferous (Conti *et al.* 1977). The formation itself comprises up to 150 m of conglomerates, coarse and fine-grained sandstones, siltstones, and sandy-conglomerate cycles (Conti *et al.* 1977). The Butterloch-Bletterbach section, from where the Val Gardena footprints were collected (Conti *et al.* 1977), lies approximately 150 km south-west of the Italian-Austrian-Slovenian border junction. Sediments comprise reddish, green, grey, and yellow siliciclastic sandstones with occasional calcareous horizons, alternating with muddy sandstones and clays. Gypsum layers are found throughout the sequence, reflecting an increasingly arid climate, whilst large, isolated gypsum nodules dominate the lower 30 m of the succession (Conti *et al.* 1977). Sedimentary structures include salt-crystal moulds, raindrop imprints, infilled desiccation cracks, ripple marks, and localised cross-bedding. The only faunal elements recorded, other than vertebrate trackways, are terrestrial plant fragments. The Val Gardena Sandstone in north-eastern Italy is overlain by marine sediments of the Bellerophon Formation, a deposit of carbonates and evaporites representing a gradual marine transgression during the latest Permian (Conti *et al.* 1977).

Trackway locality	Ichnotaxon: Amphisauropus	Limnopus (Limnopus)	Limnopus (Batrachichnus) plainvillensis	Limnopus (Batrachichnus) salamandroides	Notalacerta	Varanopus	Rhynchosauroides	Chirotherium	Dromopus	Dimetropus	Hyloidichnus	Ichniotherium	Erpetopus	Tambachichnium	Lissamphibia	Amniota	Total
Alveley Member, UK		20	26	157						8	1	1			177	36	213
Earp Formation, New Mexico		1		8					9						9	9	18
Hueco Formation, New Mexico	9	12		131					101	102	158		4		143	374	517
Abo Formation, New Mexico	24	22		90		2			99	15	27		4		112	171	283
Sangre de Cristo Formation, New Mexico	10	18		1		1			40	3	9	2			28	65	93
Choza Formation, Texas	1					8			36				58		0	103	103
Tambach Formation, Germany (percentages)						1				28		70		1	10	90	100
Standenbühl Formation, Germany	61	5		36		8			65	5	40				41	181	222
Val Gardena Sandstone, Italy	17	2			2	2	53	2	90	1					2	167	169
Provencal Basins, France	24			42		25			60	6	71				42	186	228

TEXT-FIG. 5.4. Ichnofaunal count at trackway localities across Europe and North America. Unidentified specimens are not included. Numbers of Lissamphibia and Amniota based upon trackmaker identification using synapomorphy-based, coincidence, and phenetic correlation methods (Olsen 1995; Carrano and Wilson 2001). Data from: Alveley Member: Tucker and Smith (in press). Earp, Hueco, Abo and Sangre de Cristo formations: Lucas (1993); Hunt *et al.* (1993, 1994 *a*, *b*, 1995*a*); Lucas *et al.* (1994, 1998); Haubold *et al.* (1995); Lucas and Heckert (1995); Schult (1995*a*, *b*); Hunt and Lucas (1998); Lucas *et al.* (2001); Lucas and Heckert (unpublished data). Choza Formation: Haubold (1971*a*); Haubold and Lucas (2001). Tambach Formation: Haubold (1998); Eberth *et al.* (2000). Standenbühl Formation: Fichter (1983*a*, *b*, *c*, 1984); Boy and Fichter (1988); Haubold and Stapf (1998). Val Gardena Formation: Conti *et al.* (1977). Provencal Basins: Demathieu *et al.* (1992).

THE DEVELOPMENT OF TERRESTRIAL TETRAPOD COMMUNITIES THROUGH THE LATE PALAEOZOIC

Following a systematic revision of ichnofaunas from the above localities, the ichnological data were analysed with the use of synapomorphy-based, phenetic and coincidence correlation techniques (Olsen 1995; Carrano and Wilson 2001) to determine the relative proportions and abundance of total-group lissamphibians and total-group amniotes within each assemblage (Fig. 5.4). This correlation method is based upon linking trackways to trackmakers using shared derived characters of biotaxa that are identifiable in trackways, and comparisons of morphology and stratigraphical occurrences provide further correlatory data. Figure 5.2 illustrates the relative proportions of lissamphibians (Fig. 5.1) within Late Palaeozoic terrestrial communities in terms of both the number of recorded biological taxa (data derived from taxonomic richness diagrams, Fig. 5.3), and the relative abundance of actual individuals (from trackway data, Fig. 5.4). Whilst taxonomic richness diagrams indicate a gradual decrease in the proportion of lissamphibians within terrestrial communities through the Late Palaeozoic, trackway data demonstrate that in terms of the relative abundance of individuals within these communities, lissamphibians formed the principal component of terrestrial communities throughout the Carboniferous, and to a lesser extent, the Early Permian. Thus, trackway data provide information relevant to community analysis that traditional studies, based upon taxonomic richness diagrams, would not recognise. For instance, although patterns of biological taxon diversity indicate an extinction event during the Artinskian (Early Permian), an incident that affected both lissamphibians and amniotes, trackway data emphasise the negative effect on lissamphibians, whilst recognising that lissamphibian abundance was already in decline long before the Artinskian. It appears that this extinction event was not as central to the phenomenon of lissamphibian decline as would be interpreted from taxonomic richness diagrams. Thus, ichnofaunal diversity within these trackway assemblages indicates progressive clade displacement of stem-lissamphibians by members of the total-group Amniota within terrestrial habitats during the Late Palaeozoic. Kitchell (1985, p. 97) defined taxon displacement as the 'numerical dominance, in terms of taxonomic richness, of one taxon over another, resulting from some motive force'. This force may be the direct result of competitive interaction between the two taxa, or it may involve environmental or ecological factors that cause the taxa to diversify or decline independently of one another. By comparison, taxon replacement is defined as the 'opportunistic diversification by surviving species following an extinction event' (Kitchell 1985, p. 97) and therefore potentially involves little or no interaction between the two groups of taxa.

It is of course possible that the observed displacement is merely artefactual. Factors such as the effects of taxonomy (in particular, the taxonomic level to which the data are compiled), and biases in preservation, perhaps influenced by depositional environments, may significantly affect the patterns observed. Adopting the following precautions reduces the effects of artefactual data: 1) all trackway

data considered have been subject to a taxonomic revision by the present author. This follows a study of much of the original trackway material, and only trackway assemblages that are comprehensively and sufficiently described and figured in the literature were used to supplement these data. 2) the trackway assemblages used in this study all originate from similar depositional environments, with the exception of the Tambach Formation assemblage, which can be expected to contain slightly higher proportions of amniotes than otherwise expected due to the more 'upland' position. Modes of preservation are consistent throughout these assemblages, and trackways from any other than the surface or very top levels of preservation (undertracks and overtracks) are disregarded. As the trackway data still show an increase in amniote forms and a coincident decrease in lissamphibians, the observed displacement is considered to be 'real' and not artefactual. Consequently, a number of hypotheses regarding the causes, or 'motive forces' instigating this observed faunal turnover are here tested, to investigate the patterns and processes involved. Four potential, and non-mutually exclusive, models are identified.

Model 1: Direct competition between stem-lissamphibians and early amniotes

Two taxa are said to be in competition if an increase in abundance by either one harms the other (Benton 1996*a*). In this case, it is hypothesised that an increase in the abundance of amniotes, in terms of both taxonomic richness and numbers of individuals, was significant in instigating and sustaining stem-lissamphibian decline. However, before a hypothesis of direct competition can be fully tested, a number of criteria, as outlined by Benton (1987, 1996*a*, *b*) must be fulfilled. The purportedly competing taxa must share habitats, geographical distribution, diet and other resources, and must be of comparable body size. In addition, taxonomic richness and species abundance diagrams should show appropriate, corresponding patterns of diversification and decline within the two potentially competing taxa (e.g. Benton 1996*a*; Sepkoski 1996). Trackways directly provide all of these data with a relatively high level of reliability. An exception is dietary information, which can be hypothesised from the evidence of community structure that comprehensive trackway collections provide, and so can also be effectively used to test hypotheses of competition.

Criteria for direct competition

Habitats

The taxa under consideration in this study must, to a certain extent, have occupied the same habitats, as their trackways are found together within discrete sedimentary horizons. Trackways are particularly informative in ascertaining preferred habitats as they confirm the presence of given taxa within their living environment. Stem-lissamphibians and amniotes occupied a relatively wide range of Late Palaeozoic habitats, both terrestrial and aquatic (Olson 1971; Benton 1979, 1993, 1996*a*, *b*; Milner 1980; Carroll 1988). Consequently, although the habitats of members of the two clades may have

overlapped in part, as shown by the co-occurrence of their trackways, either clade may have occupied areas in which the other was absent and in which direct competition between the two taxa was impossible.

Disparities between amniotes and stem-lissamphibians in terms of habitat areas may have given amniotes a competitive advantage over stem-lissamphibian taxa, thereby partly accounting for the pattern of taxon displacement observed here. Olson (1971) proposed that Permo-Carboniferous tetrapod communities inhabited four environmental sub-zones (and therefore four feeding habitats): fully aquatic, semi-aquatic (based mainly in water with occasional terrestrial excursions), semi-terrestrial (based predominantly on land, but relying upon aquatic food sources), and fully terrestrial. The feeding habits of the first three groups are interlinked, and ultimately depend upon aquatic sources of nutrition at the base and lower levels of the food chain. These faunal complexes included stem-lissamphibians, and semi-aquatic and semi-terrestrial early amniotes (Olson 1971). In comparison, the morphology and feeding behaviour of more terrestrial amniotic forms, such as the carnivorous 'pelycosaurs' and captorhinomorphs, suggests that they were less directly dependent upon aquatic food sources, perhaps feeding upon smaller, herbivorous terrestrial and semi-terrestrial tetrapods (Olson 1971; Reisz 1986). They were therefore more readily able to exploit the terrestrial environment, filling ecological niches that were not available to those taxa that required a constant nearby water source for food. Although all of the trackway assemblages upon which this analysis is based are characteristic of fluvial/alluvial or similar environments, and therefore represent tetrapod communities near to water sources, the ability of amniotes to colonise habitats away from water is important, nevertheless, as these terrestrial forms were able to visit riparian environments, whilst maintaining a wider habitat area.

Geographical distribution

Taxa at individual trackway localities clearly overlapped in geographical distribution, as confirmed by the co-occurrence of their footprints. Tracksites across North America and Europe, including those used in this study, demonstrate a remarkably conservative diversity of ichnotaxa, especially during the Permian (Haubold 1996, 2000; Haubold and Lucas 2001). Skeletal material from North America and Europe also indicates a cosmopolitan early terrestrial tetrapod fauna, due to the faunal interchange between present day continents made possible by the single, Late Palaeozoic Laurasian supercontinent (Milner and Panchen 1973; Benton 1979, 1993). Although the generic and specific identity of trackmakers within these different trace fossil assemblages may vary slightly, a detail that cannot be either proven or disproven given the current state of information regarding the correlation of trackways with trackmakers (e.g. Schult 1995*a*; Carrano and Wilson 2001; Chapter 4), lissamphibian and amniote trackways remain distinguishable by the number of digits on the manus. Trends in the abundance and proportions of lissamphibians and amniotes in any given trackway assemblage can be

traced despite potential variations in generic or familial diversity within these two clades. The co-occurrence of terrestrial lissamphibians and amniotes in these assemblages is therefore indisputable.

Diet and shared resources

As discussed above, the trackmakers represented at individual trackway localities must have shared one particular habitat, although the full range of habitats of any given taxon most likely extended beyond this. Nevertheless, competition within this partially overlapping range may have been enough to affect radiation and speciation rates within one or both clades. In terms of diet, Late Palaeozoic lissamphibians and amniotes were inextricably linked (Olson 1971; Milner 1980). Olson (1971) postulated that the predominant food web structure for early tetrapods within fluvial-alluvial and deltaic communities relied upon larger, carnivorous amniote forms feeding upon stem-lissamphibians and smaller aquatic amniotes, which in turn consumed a mixture of aquatic plants and invertebrates. It therefore follows that the radiation and decline of these groups were interdependent, and this is illustrated by the almost simultaneous radiation in the diversity of stem-lissamphibians and primitive amniotes during the Late Carboniferous (Fig. 5.3). However, the appearance of herbivorous and insectivorous amniotes in the Early Permian (Reisz 1986) enabled a second type of trophic structure to evolve (Olson 1971), thereby liberating amniotes from their dependence upon stem-lissamphibians for food. Larger, carnivorous amniotes fed predominantly upon the smaller herbivores and insectivores, reducing the connection between amniote and stem-lissamphibian food chains in these communities. Thereafter, the radiation and decline of stem-lissamphibians and amniotes were no longer interlinked, as demonstrated by taxonomic richness diagrams for the Permian (Fig. 5.3). This independence of aquatic food sources may have constituted one of the 'key adaptations' of amniotes that enabled their rapid radiation following the end-Artinskian extinction event.

Body size

Estimates of early tetrapod body sizes have been taken from the database compiled by Benton (1996*a*), with reference to body size estimates in the chapters of Benton (*Reptilia*) and Milner (*Amphibian-Grade Tetrapoda*) in *The Fossil Record 2* (Benton 1993). Three size categories, based upon snout-vent length, are considered: small (less than 150 mm); medium (150 mm–1.5 m); and large (longer than 1.5 m). These categories are purposefully broad to allow for size variations among species within a family, and size changes throughout growth (Benton 1996*a*). Amongst the clades Lissamphibia and Amniota, there is a significant overlap in body size amongst smaller, or juvenile, amniote taxa and the majority of stem-lissamphibians. However, many amniote taxa are larger than stem-lissamphibian taxa. It therefore appears that in the same sense as amniote habitats extended beyond those of stem-lissamphibians, the range of body size in amniotes extended beyond that of stem-lissamphibians. These larger amniote forms were not experiencing competition from stem-

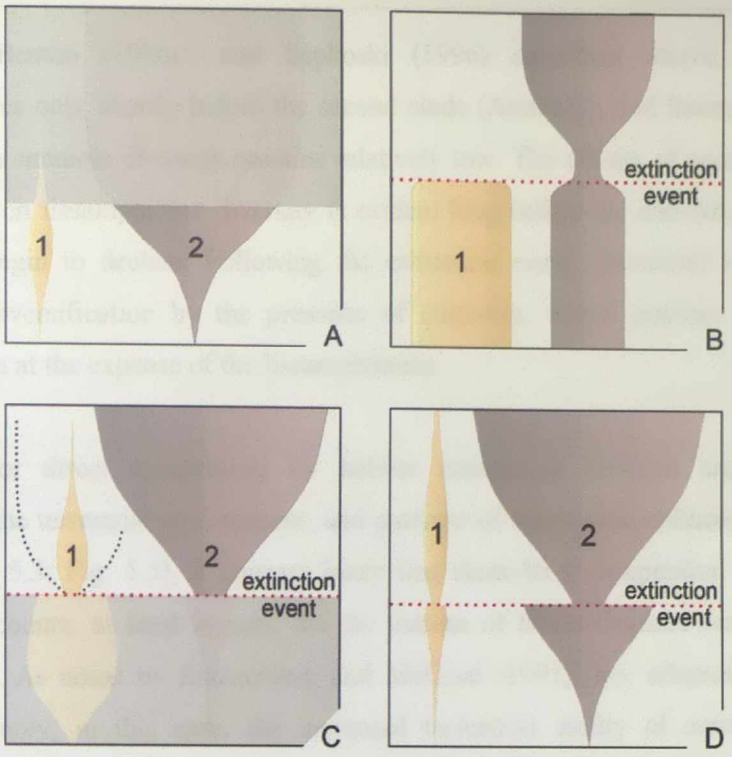
lissamphibians (or indeed, any other taxa), and so were unrestricted in their radiation, providing sufficient food sources were available.

Patterns of taxonomic richness and species abundance

Patterns of taxonomic richness among terrestrial stem-lissamphibians and total-group amniotes during the Late Carboniferous and Early Permian have been compiled (Fig. 5.3) based upon a new phylogenetic analysis (Ruta *et al.* 2003; Fig. 5.2), and the combined phylogenetic analyses of Reisz (1986), Laurin (1993), Gauthier (1994), Laurin and Reisz (1995), and Lee (1995), in conjunction with a Late Palaeozoic tetrapod family census taken from the literature (Carroll 1988; Benton 1993; Milner 1994; Milner and Sequeira 1994, 1998; Clack 1994, 1998, 2001, 2002*b*; Lombard and Bolt 1995, 1999; Coates 1996). Patterns within the resulting spindle diagram are closely comparable to the solution for a coupled logistic equation modelling competitive clade displacement depicted by Sepkoski (1996, fig. 9.8, p. 228; Fig. 5.5A). This figure represents a pattern of clade displacement whereby two clades originate simultaneously (amniotes only shortly after lissamphibians in this case). Members of the first clade (lissamphibians) have a lower rate of diversification and a lower maximum ('equilibrium') diversity than those of the second clade (amniotes), and therefore the first clade is able to radiate as long as diversity within the second clade remains low. Once diversity and abundance increase within the second clade, the abundance of the first clade declines.

Following the extinction of non-marine vertebrates at the end of the Artinskian, as noted by Benton (1989), and illustrated by taxonomic richness patterns (Fig. 5.3), both clades re-diversify, but lissamphibians do not diversify at the same rate as they would in the absence of a high diversity and abundance of amniotes. The consequent patterns of taxonomic richness more closely match Sepkoski's (1996) solution for a coupled logistic equation modelling the effects of a mass extinction on clade displacement (fig. 9.9, p. 229; Fig. 5.5C). Immediately before the mass extinction, the first clade is in decline, as a result of displacement by members of the second clade. After the mass extinction, both clades re-diversify, although the first clade is restricted by the presence of the second clade. This is also comparable with Benton's (1996*a*) model of 'non-competitive adaptive radiation' (Benton 1996*a*, fig. 8.1, 4, p. 188; Fig. 5.5B), whereby the members of the second clade (e.g. Amniota) possess a 'key adaptation', or set of adaptations, enabling them to successfully radiate in the aftermath of extinction. Members of the first clade (e.g. Lissamphibia) lack such adaptations and therefore do not radiate to the same extent. This model does not implicitly involve competition, but, in this case, it is probable that lissamphibians were restricted in re-diversification by amniote dominance.

Figure 5.5D illustrates a new model for the displacement of terrestrial lissamphibians by terrestrial amniotes, based upon data from trackway material (Fig. 5.2), taxonomic richness diagrams (Fig. 5.3),



TEXT-FIG. 5.5. Models of biotic replacement. Grey areas not pertinent to present discussion. (A) Two clades originate simultaneously. Members of the first clade (e.g. lissamphibians) have a lower rate of diversification and a lower maximum ('equilibrium') diversity than those of the second clade (e.g. amniotes), and therefore the first clade is able to radiate as long as diversity within the second clade remains low. Once diversity and abundance increase within the second clade, the abundance of the first clade declines. After Sepkoski (1996). (B) Model of 'non-competitive adaptive radiation', whereby the members of the second clade possess a 'key adaptation', or set of adaptations, enabling them to successfully radiate in the aftermath of extinction. Members of the first clade lack such adaptations and therefore do not radiate to the same extent. After Benton (1996*a*). (C) Model illustrating the effects of mass extinction on clade displacement. Immediately before the extinction, the first clade declines as a result of displacement by members of the second clade. After the extinction, both clades re-diversify, although the first clade is restricted by the presence of the second clade. After Sepkoski (1996). (D) A new model for the displacement of terrestrial lissamphibians by terrestrial amniotes, based upon trackway data (relative abundance of individuals; Fig. 5.1), taxonomic richness diagrams (diversity of taxa; Fig. 5.3), and the models of Benton (1996*a*) and Sepkoski (1996). The first clade (Lissamphibia) originates only shortly before the second clade (Amniota), and lissamphibians are able to radiate for as long as amniote diversity remains relatively low. The effects of amniote radiation, and associated competition, on lissamphibian diversity are evident long before the Artinskian extinction event, as the Lissamphibia begin to decline. Following the extinction event, terrestrial lissamphibians are restricted in their re-diversification by the presence of amniotes, which possess 'key adaptations' (see text) enabling them to radiate at the expense of the lissamphibians.

and the models of Benton (1996*a*) and Sepkoski (1996) described above. The first clade (Lissamphibia) originates only shortly before the second clade (Amniota), and lissamphibians are able to radiate for as long as amniote diversity remains relatively low. The effects of amniote radiation and associated competition on lissamphibian diversity is evident long before the end-Artinskian extinction, as the Lissamphibia begin to decline. Following the extinction event, terrestrial lissamphibians are restricted in their re-diversification by the presence of amniotes, which possess 'key adaptations' enabling them to radiate at the expense of the lissamphibians.

Given the evidence for direct competition for habitat occupation between amniotes and stem-lissamphibians within the terrestrial environment, and patterns of taxonomic richness illustrated by the spindle diagrams (Fig. 5.3; Fig. 5.5), it appears likely that clade-level competition between amniotes and lissamphibians accounts, at least in part, for the pattern of taxon displacement observed within trackway assemblages. As noted by Rosenzweig and McCord (1991), key adaptations possessed by the second clade (notably, in this case, the increased terrestrial ability of amniotes) remove the selective advantage for individuals of the first, older clade to deviate from their ancestral species; speciation is therefore reduced within the first clade.

Model 2: Radiation of amniotes through 'key adaptations'

Expansion into new ecological niches, involving no biotic interaction, has been suggested as the primary basis for the majority of tetrapod radiations (Benton 1996*a*, *b*). Indeed, following the vertebrate transition to land in the Late Devonian (Coates 1996; Clack 1997, 2002*a*), a multitude of new habitats, with plentiful food sources and a conspicuous lack of competition from other taxa, became available to suitably adapted groups. It is here hypothesised that rapid adaptive radiation similarly occurred within the amniotes, as their improved terrestrial ability (e.g. locomotion, feeding patterns, and in particular, reproduction, following the appearance of the amniotic egg) enabled the exploitation of new habitats unavailable to stem-lissamphibians. Speciation rates increased, thereby expanding the number of individuals present within a given community. This would not necessarily involve a decline in stem-lissamphibian diversity or abundance, but would merely serve to increase the number of amniote taxa within terrestrial habitats, thereby altering the proportion of the two clades within terrestrial faunal assemblages. Alternatively, the advantages bestowed upon amniotes by these improved terrestrial abilities may have reflected 'key adaptations' (Benton 1987, 1996*a*, *b*; Rosenzweig and McCord 1991; Purnell 2001) that allowed amniotes to directly out-compete stem-lissamphibians.

A number of hypotheses have been put forward for the driving forces behind the initial tetrapod transition to land. Martin and Nagy (1997) postulated that aquatic forms were disadvantaged by

hyperoxia and the resulting poor water quality during the Carboniferous, together with a change to a warmer, more arid climate, encouraging the development of terrestrial abilities in stem and primitive crown-group tetrapods. These capabilities were improved upon by stem-lissamphibians, but were more enhanced in amniotes, allowing further exploitation of the land during the Late Carboniferous and Permian, and expansion into niches made newly available by an increased amniote capacity for terrestrial locomotion, breeding, and water retention (e.g. Carroll 1988; Frolich 1997; Graham *et al.* 1997). This expansion was promoted by abundant atmospheric oxygen, particularly during the Carboniferous (Grossman 1994; Veevers 1994; Graham *et al.* 1997), plentiful food in the form of plants and arthropods, little competition for space, and reduced egg predation. Comparison of extant reptiles and amphibians indicates that the ability of amniotes to fully exploit these beneficial conditions was much greater than that of lissamphibians. Recent amniotes are able to maintain hydration out of water, forage on the land, and reproduce within a terrestrial environment, all with much greater success than amphibians, a few species of which may attain efficiency in one of these areas only through specialised adaptations (Martin and Nagy 1997). Amniote expansion and the subsequent diversification of carnivorous forms presented a higher risk of predation to small aquatic, and in particular, terrestrial stem-lissamphibians; a factor that may have been significant in their decline.

Potential 'key adaptations' in amniotes facilitating expansion

The vertebrate transition to land was facilitated by a number of adaptations enabling partial terrestriality in the earliest tetrapods. These innovations involved changes in the locomotory, support, reproductive and respiratory systems, as well as alterations in diet, water balance and sensory input (e.g. Clack, 2002*a*; Carroll, 1988). However, although early tetrapods and stem-lissamphibians developed terrestrial adaptations, these were greatly improved in amniotic forms, enabling the earliest amniotes to exploit terrestrial environments with more success than both their tetrapod ancestors and the stem-lissamphibians.

Terrestrial locomotion

Higher levels of ossification within amniote skeletons (Reisz 1986; Carroll 1988; Liem *et al.* 2001) increased the ability of amniote limb bones to support body mass during terrestrial excursions. In addition, amniotes exhibit increased terrestrial locomotory agility, as indicated by a number of skeletal adaptations. For example, limb proportions in amniotes are more suitable for terrestrial locomotion, providing a larger propulsive force from the hindlimbs (Reisz 1986; Graham *et al.* 1997), as are changes towards more upright gaits, as indicated by trackway evidence. Other adaptations towards improved terrestriality, involving soft-part anatomy, include the presumed presence of stretch receptors associated with the axial and appendicular muscles (Carroll 1988), and the mechanical support and trauma protection functions of amniote skin (Frolich 1997).

Reproduction

The appearance of the amniotic egg, which through the use of a system of extra-embryonic, permeable membranes enabled egg-laying within terrestrial environments, allowed amniotes to become less reliant upon water sources for reproduction. Risks of predation by other amniotes, and in particular, fish – the most common predators upon extant amphibian eggs (Kats and Ferrer 2003) – was greatly reduced, as was the risk of dehydration within potentially unstable aquatic environments (Romer 1957, 1967; Stewart 1997). Following hatching, terrestriality was further enabled by the direct development of young (Romer 1967; Carroll 1988), thereby eliminating the aquatic larval stage at which the risk of predation for small forms was highest (Olson 1971). The possibility of internal fertilisation within amniotes has been suggested (Carroll 1988), although no evidence of copulatory organs appears in the fossil record.

Aerial respiration capabilities

In comparison to the bimodal respiratory systems of stem-lissamphibians (Holmes 2000; Clack 2002*a*), amniotes possess fully functional lungs, suitable for both efficient oxygen uptake and carbon dioxide release (Kardong 1998; Liem *et al.* 2001; Clack 2002*a*). As a result, the volume of water loss through the lung membranes during aerial respiration is reduced (Kardong 1998), and terrestrial excursions can therefore be lengthened without requiring a steady water supply.

Diet

Whilst stem-tetrapods and many stem-lissamphibian taxa exhibited relatively large, broad heads, with long sharp teeth adapted for the consumption of other vertebrates (both fish and tetrapods), many early amniotes, with small, narrow skulls, possessed a tooth structure and inferred jaw musculature indicative of insectivory (Carroll 1988). Herbivorous forms, notably the early synapsid or 'pelycosaurian' edaphosaurs (Reisz 1986) also appeared among the Amniota during the Late Carboniferous, representing further divergence into varied modes of feeding. The increased abundance of terrestrial plants during the Late Palaeozoic (Knoll *et al.* 1984; Kenrick and Crane 2000) conceivably provided more food for these herbivorous forms, aiding their expansion. Meanwhile, other early synapsids (for example, sphenacodontid 'pelycosaurs') improved upon early tetrapod carnivorous adaptations with the development of more massive skulls and specialised dentition (Reisz 1986).

A possible factor in the decline of terrestrial lissamphibians during the Permian, related to dietary habits, is an increase in predation risk resulting from amniote expansion and consequent radiation. The eggs and larvae of amphibians are particularly vulnerable to predation by both fish and amniotes, as shown by a recent study of extant species (Kats and Ferrer 2003). A hypothetical Late Palaeozoic trophic web outlined by Olson (1971) suggests that stem-lissamphibian eggs and aquatic larvae,

together with small, predominantly aquatic stem-amniote species (particularly microsaurs and lysorophids), formed the base and lower levels of the food chain in most scenarios, with small- and medium-sized herbivorous amniotes (such as edaphosaurs) at the base of the food chain within fully terrestrial environments. Most adult stem-lissamphibians were also open to predation by medium-sized, carnivorous amniotes (such as the sphenacodont *Dimetrodon*) within semi-terrestrial habitats. The expansion of amniotes into new adaptive zones, following their initial radiation, would therefore have greatly increased the levels of predation upon all stem-lissamphibians, having an impact upon the trophic web at several different levels.

Water requirements and retention

Extant amphibians are highly dependent upon water. When fully hydrated, water accounts for up to 83 per cent of body mass, in comparison to 70 per cent in reptiles and mammals (Martin and Nagy 1997). The typical amphibian daily water uptake reaches up to 360 per cent body mass, whilst up to 160 per cent body mass of water is lost through the skin per day (Martin and Nagy 1997), an amount which increases in drier, warmer environments due to high rates of evaporation. The majority of this water gain and loss occurs through the skin, which forms the primary osmoregulatory organ in recent lissamphibians. The skin is highly specialised for both gas and water exchange, having a high fluid permeability (Bentley 1966; Frolich 1997). Extant lissamphibians are therefore able to heavily rely upon cutaneous respiration, but this is only possible in moist environments (Carroll 1997), a factor that precludes lissamphibians from occupying fully terrestrial habitats. In addition, the duration of terrestrial ventures in amphibians is limited by the accumulation of nitrogenous waste products in the blood plasma, caused by the inability of amphibians to excrete concentrated urine on land (Carey and Alexander 2003), and the amphibian requirement for constantly moist skin for effective gas exchange. However, Late Palaeozoic stem-lissamphibians were covered with a mixture of both ventral dermal gastralia and thinner dorsal scales (Holmes 2000), and so it is postulated that these forms may have been less reliant upon cutaneous gas exchange then their recent descendants.

Extant reptiles demand only 1–5 per cent of typical amphibian water requirements, and maintain lower rates of water loss by excreting solid faecal pellets of uric acid, so enabling dry precipitation of sodium and potassium ions that would otherwise require water to expel in dissolved form. Additionally, the keratinised outer skin layer of amniotes is easily hydrated and is used, together with a lipid coating, to regulate water exchange in different environments (Frolich 1997). The amniotic ability to achieve water balance without a constant source of ambient moisture is further facilitated by their choice of high water content foods, low water loss rates, and the ability to store up to 30 per cent of body mass in the form of water in the urinary bladder (Martin and Nagy 1997).

These combined adaptations pose great advantages over amphibians in the exploitation of terrestrial environments. 'Key adaptations' in amniotes enabled this group to improve upon the terrestrial abilities of the stem-lissamphibians, and thereby exploit a wide range of habitats that were previously unoccupied. The striking lack of competition for resources (in particular, space, and food after the adoption of amniote insectivory and herbivory) would have enabled amniotes to expand unrestricted into a large number of newly available niches. As intra-clade competition within amniotes reached critical levels, this would have initiated further morphological diversification within amniotes – as suggested by experimental evidence (Schluter 1994) – and more niches would become available as a result. Lissamphibians, in comparison, were constrained by a lack of adaptations for fully terrestrial habits and were accordingly inhibited in adaptive radiation, exhibiting low diversification rates.

Model 3: A change in preferred stem-lissamphibian habitats

In an overview of the lissamphibian fossil record, Carroll (1988) noted that whilst Late Carboniferous and Early Permian stem-lissamphibians were primarily terrestrial, the temnospondyls of the Late Permian and Triassic became increasingly aquatic. It is possible that stem-lissamphibians were forced to retreat to aquatic habitats by the increasing dominance of amniotes within the terrestrial environment. Indeed, a similar pattern of habitat preference is seen within microsaurs (Carroll and Gaskill 1978). During the Late Carboniferous, microsaurs were dominant as stem-amniotes within terrestrial habitats, but were displaced by crown-group forms by the latest Carboniferous and Early Permian. In comparison, microsaurs of the Permian were primarily long bodied, short limbed, aquatic forms that did not come into contact with terrestrial crown-group amniotes (Carroll and Gaskill 1978). It is possible that this change in morphology and preferred habitat represents an evolutionary response by microsaurs to the increased competition from crown-group amniotes, and that stem-lissamphibians were similarly affected. Trackways of aquatic animals would not be evident in the terrestrial assemblages considered here – and, indeed, are very infrequently preserved in any case – so these tracksites would not trace any change in stem-lissamphibian habitat preferences towards aquatic environments.

Complications in this observed pattern arise, however, when the effects of the end-Artinskian extinction event are considered. Figure 5.3 illustrates taxonomic richness diagrams of lissamphibians and amniotes considered in terms of habitat preference (terrestrial and aquatic). These indicate that the change in stem-lissamphibian habitats, which may initially appear to represent an evolutionary response to amniote dominance, was instead most likely a result of differential lissamphibian re-diversification rates within terrestrial and aquatic environments following the near extinction of the clade at the end of the Artinskian. As noted above, the subsequent radiation of lissamphibians in terrestrial habitats was probably restricted, as a result of either the competitive dominance of amniotes,

or the lack within stem-lissamphibians of key adaptations enabling rapid radiation in terrestrial environments. In contrast, the radiation of aquatic stem-lissamphibians, although hampered by the presence of amniotes, was affected to a much lesser degree. This accounts for the apparent preference for aquatic habitats demonstrated by Late Permian and Triassic temnospondyls. The observed change in stem-lissamphibian habitats was not directly a result of a competitively driven evolutionary response to amniote dominance by the temnospondyls, but rather the consequence of extrinsically influenced, non-competitive, differential radiation following an extinction event.

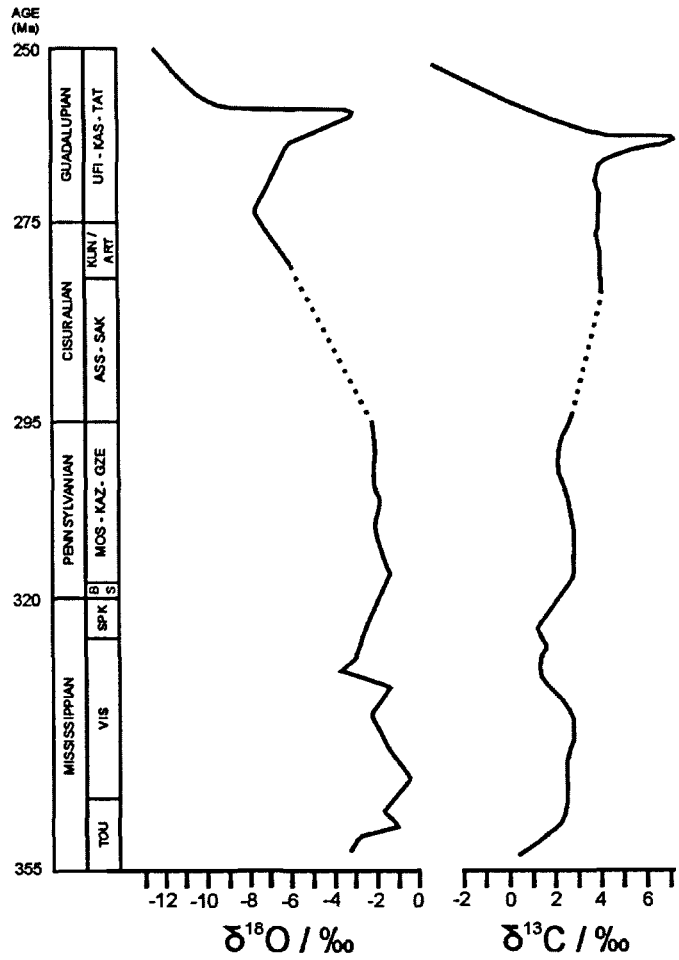
Model 4: Climate change

Climatic zonation is the most influential factor affecting latitudinal faunal provinciality at the present day, with a general increase in biodiversity towards the equator. The presence of the single supercontinent Pangaea during the Late Palaeozoic would have affected climatic zonation, particularly with the amalgamation of zoned atmospheric circulatory systems, producing a globally more uniform climate that would account for the cosmopolitan nature of early terrestrial tetrapod faunas as charted by Milner and Panchen (1973). However, atmospheric composition changed dramatically during the Late Palaeozoic, and this is likely to have had a significant influence upon terrestrial vertebrate evolution and development. Geological indicators of global temperature, such as marine carbonate mineralogy, composition of benthic communities, palaeosol structure, and the presence or absence of dropstones, red-beds, coals, and caliches, indicate that northern Pangaea underwent a period of intense cooling during the Permian, coupled with increasing aridity (Beauchamp 1994). This evidence is supported by carbon and oxygen isotope data (Grossman 1994; Worsley *et al.* 1994), and models taking Pangaean palaeogeography, palaeotopography and the eccentricity of Earth's palaeo-orbit into account (e.g. Crowley 1994; Kutzbach 1994). Atmospheric oxygen levels were particularly high during the Late Carboniferous, and declined during the Permian (Graham *et al.* 1997; Beerling *et al.* 2002; Fig. 5.6), with a coincident rise in atmospheric carbon dioxide levels (Worsley *et al.* 1994; Veevers 1994; Graham *et al.* 1997; Fig. 5.6). Laurasia extended across the equator and into northern latitudes in the Early Carboniferous, and subsequently migrated approximately 50 degrees northwards during the Carboniferous and Permian (Lottes and Rowley 1990; Ross and Ross 1990; Scotese and McKerrow 1990; Witzke 1990; Ziegler, P. A. 1990; Beauchamp 1994; Golonka *et al.* 1994; Fig. 5.7). This engendered increasing aridity throughout Laurasia (Witzke 1990; Ziegler, A. M. 1990; Francis 1994) and a proposed decrease in average global surface temperatures (Ross and Ross 1990). This combination of changes in atmospheric composition and global temperatures would have benefited newly terrestrial amniotic forms, giving them an advantage (either competitive or non-competitive) over stem-lissamphibians, which in turn were negatively affected by increasing aridity.

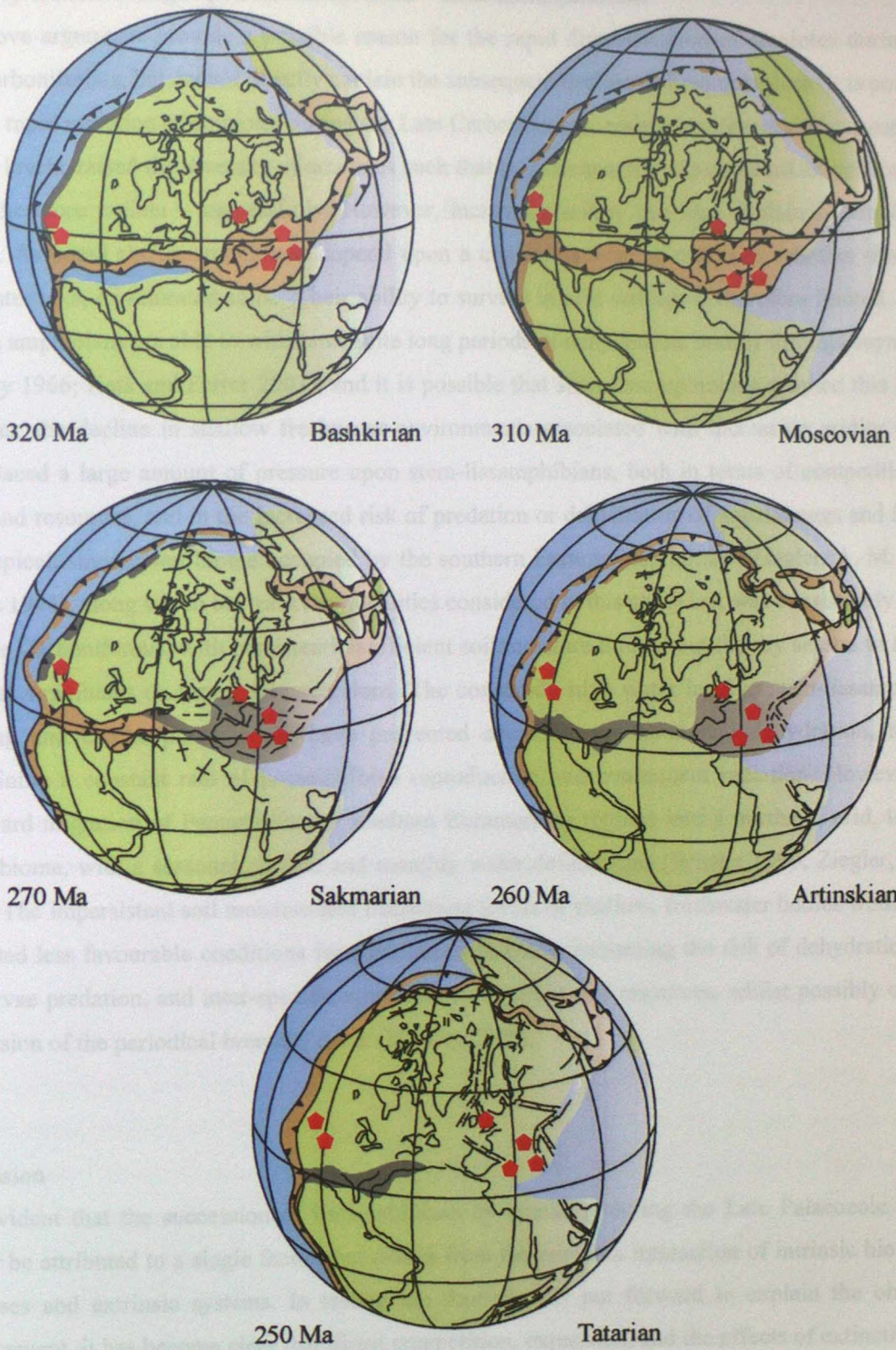
The trackway localities considered in this study all fall within close range of the Late Palaeozoic palaeoequator (Fig. 5.7), and so were equally affected by climate changes related to both atmospheric composition and Pangaean migration. At these latitudes, climates during the Carboniferous and Early Permian were hot and humid, optimal for stem-lissamphibians, and were consistently warm enough for early amniotes throughout the Late Palaeozoic.

Effects of climate change upon terrestrial biota – amniotes

Hyperoxic conditions during the Carboniferous may have been a factor in the rapid radiation of early terrestrial amniotes during this interval. The improvements in terrestrial adaptations in these taxa, which gave them a competitive or non-competitive advantage over stem-lissamphibians, would have been positively affected by an increase in atmospheric oxygen levels, and this could explain early amniote success. Four particular key adaptations were potentially affected: aerial respiration; water retention abilities; improved terrestrial locomotion; and diet. For example, an increase in oxygen supply to the muscles enables greater power in locomotion, and sustained exercise. Metabolic recovery from anaerobic activity is hastened, and aerobic endurance is higher (Graham *et al.* 1997). Secondly, hyperoxia has been suggested as the cause for the appearance of gigantic Carboniferous arthropods and winged insects (Carroll 1988; Graham *et al.* 1997). The early amniote families Protorothyrididae, Araeoscelididae and Captorhinidae, as well as some early diapsids, capitalised on this rapid radiation of large invertebrates by adopting insectivory (Carroll and Gaskill 1978; Reisz 1986; Graham *et al.* 1997). Narrower, smaller skull shapes appeared, with associated alterations in jaw attachments (Reisz 1986). This newly acquired dietary habit enabled the exploitation of previously unoccupied terrestrial niches, with abundant food sources allowing relatively rapid adaptive radiation of insectivorous groups. Finally, as noted above, the respiratory systems of juvenile stem-lissamphibians, as bimodal breathers with both lungs and gills (Holmes 2000; Clack 2002*a*), functioned more efficiently in water than on land. Gills are used primarily for carbon dioxide release in modern bimodal breathers (Graham *et al.* 1997), and the lungs are not as well adapted for oxygen uptake and carbon dioxide release as those of amniotes. Early amniotes would therefore have had a slight advantage over stem-lissamphibians in aerial respiration, and may consequently also have benefited more from an increase in atmospheric oxygen levels. Stem-lissamphibians are thought to have respired cutaneously, and this method of breathing is restricted to well-oxygenated habitats (Liem *et al.* 2001) that declined with decreasing oxygen levels during the Permian. However, it should be noted that this method of gas exchange was secondary to breathing using the lungs (Holmes 2000). Therefore, any amniote advantage over stem-lissamphibians in terms of aerial respiration would probably have remained slight.



TEXT-FIG. 5.6. Oxygen and carbon stable isotope stratigraphies for the Carboniferous and Permian. Carboniferous data based upon brachiopod shell calcite from North America; Permian data based upon brachiopod shell calcite from West Spitsbergen. Dotted lines indicate uncertainty. Compiled from Mii *et al.* (1997, 1999). Stratigraphic abbreviations as for Fig. 5.3.



TEXT-FIG. 5.7. Reconstruction of continental positions during the Carboniferous and Permian (adapted from Ziegler, P. A., 1990). Red pentagons denote trackway localities.

Effects of climate change upon terrestrial biota – stem-lissamphibians

The above arguments provide a possible reason for the rapid diversification of amniotes during the Late Carboniferous, but cannot directly explain the subsequent decline of lissamphibians. It is possible that the rapid radiation of amniotes during the Late Carboniferous, assisted by favourable atmospheric oxygen levels, raised the diversity of amniotes such that stem-lissamphibians could no longer compete – and therefore radiate – successfully. However, increasing aridity can also explain lissamphibian decline. As noted above, amphibians depend upon a constant source of moisture, whether this be a freshwater lake, or saturated soils. Their ability to survive in arid settings is therefore limited. Some modern amphibians are able to withstand quite long periods of dehydration, mainly through burrowing (Bentley 1966; Kats and Ferrer 2003), and it is possible that stem-lissamphibians adopted this tactic. However, the decline in shallow freshwater environments associated with increasing aridity would have placed a large amount of pressure upon stem-lissamphibians, both in terms of competition for space and resources, and in the increased risk of predation or dehydration of aquatic eggs and larvae. The tropical, summerwet biome occupied by the southern Euramerican border (Ziegler, A. M. 1990; Francis 1994), along which the trackway localities considered in this study lay, was consistently wet in the Late Carboniferous, with persistently sufficient soil moisture throughout the dry season to sustain stem-lissamphibians on terrestrial excursions. The constantly high water level in stem-lissamphibian breeding and crèche pools would have prevented excessive predation and dehydration, thereby maintaining a constant rate of lissamphibian reproduction and consequent radiation. However, the northward migration of Pangaea forced southern Euramerican regions into a northern, arid, tropical desert biome, with a seasonal climate and monthly water deficiencies (Witzke 1990; Ziegler, A. M. 1990). The impersistent soil moisture and fluctuating levels of shallow, freshwater bodies would have presented less favourable conditions for stem-lissamphibians, increasing the risk of dehydration, egg and larvae predation, and inter-specific competition for space and resources, whilst possibly causing suspension of the periodical breeding cycle (Bentley 1966).

Discussion

It is evident that the succession of lissamphibians by amniotes during the Late Palaeozoic cannot simply be attributed to a single factor, but results from the complex interaction of intrinsic biological processes and extrinsic systems. In testing the four models put forward to explain the observed displacement, it has become clear that direct competition, expansion, and the effects of extinction and climate change may all have significantly affected the patterns of stem-lissamphibian and amniote diversity observed within successive trackway assemblages and in the body fossil record. This is supported by the evidence of taxonomic richness diagrams (Fig. 5.3), which follow two successive patterns representative of progressive clade displacement at both competitive and non-competitive levels.

At lissamphibian/amniote clade level, all criteria for a hypothesis of direct competition between these two groups are fulfilled. Initial radiation of the lissamphibians, allowing them to dominate the earliest terrestrial habitats, remained unrestricted until the abundance and diversity of amniotes increased to a level whereby competition between the two groups negatively affected the radiation of the lissamphibian clade. Key adaptations within the amniotes, particularly those facilitating life in terrestrial environments, conferred a competitive advantage on this group, and lissamphibian diversification rates and abundance declined accordingly. Meanwhile, these key adaptations related to improved terrestrial abilities enabled amniotes to exploit a larger number of ecological niches, causing further, non-competitive amniote expansion, and as a consequence, further competitive interaction with stem-lissamphibians. Following a study of the possibilities of direct competition between single families of tetrapods, Benton (1996a, b) noted that expansion is the major cause for the patterns of displacement observed in the non-marine fossil record, and the role of competition is secondary to this. Nevertheless, studies on recent amphibians show that many species are particularly vulnerable to competition from newly introduced taxa, especially those species with complex life cycles involving both aquatic larval and semi-terrestrial adult stages (Kats and Ferrer 2003). The latter study also notes that amphibian larvae grow less, and metamorphose at smaller sizes when raised in the presence of predators. This immediately gives the predatory taxa a competitive advantage over the prey taxa, further contributing to the decline of prey taxa directly caused by predation. The role of competition in the Late Palaeozoic faunal turnover should consequently not be totally discounted, although it is clear that adaptive radiation played a crucial, integral role in the faunal transition from lissamphibian to amniote dominance. Climate change, as an extrinsic influence, promoted both competitive interaction and non-competitive responses. High Carboniferous atmospheric oxygen levels encouraged early amniote radiation, whilst increasing aridity during the Permian, together with the disruption of equable equatorial climates by Gondwanan ice melt, may have acted as a further restriction upon lissamphibian terrestrial radiation. Following the end-Artinskian (Early Permian) extinction event, the effects of direct competition are reduced and amniotes rapidly rediversify and radiate within terrestrial environments, enabled by their possession of 'key adaptations' ensuring greater success in these habitats. Late Palaeozoic stem-lissamphibians did not possess such adaptations, and so their terrestrial radiation is limited, particularly in the presence of amniotes. Aquatic forms consequently dominate the stem-lissamphibian community, and amniotes dominate terrestrial habitats. In conclusion, it appears that the dynamic influence of extrinsic Earth systems and intrinsic biological processes, involving both competitive and non-competitive stem-lissamphibian and amniote interaction, produces the pattern of faunal turnover observed within trackway faunas throughout the Late Palaeozoic.

CONCLUSIONS

Late Carboniferous terrestrial palaeoenvironments and palaeoecology

The Late Carboniferous (Moscovian; Westphalian D) terrestrial ichno-assemblage of the Salop Formation extends knowledge of Palaeozoic ichnofaunas back into the mid-Late Carboniferous, a period for which little is known regarding terrestrial tetrapod communities, in comparison with well-documented Permian and Triassic faunas. Most of the ichnogenera in this mid-Late Carboniferous assemblage are otherwise restricted to the latest Carboniferous and Permian, and the assemblage produces significant stratigraphic range extensions in the amniote and stem-lissamphibian trackway record (Text-fig. 12). In addition, other ichnofaunal, floral and sedimentological data has enabled a full palaeoenvironmental and palaeoecological reconstruction of the assemblage.

This study shows that the vertebrate trackway material from the mid-Moscovian (Westphalian D) Alveley Member comprises six ichnospecies within four ichnogenera. These have been identified as *Ichniotherium willsi* (1 specimen), *Hyloidichnus? bifurcatus* (1 specimen), *Dimetropus leisnerianus* (8 specimens), *Limnopus* (*Batrachichnus*) *plainvillensis* (26 specimens), *L.* (*Batrachichnus*) *salamandroides* (157 specimens) and *L.* (*Limnopus*) *vagus* (20 specimens). The recognized ichnotaxa represent an early marginal freshwater–terrestrial tetrapod community, developed shortly after the appearance of the amniotes during the early Westphalian (Upper Bashkirian – Lower Moscovian). The ichnofauna is characterised by a high frequency and low diversity of stem-lissamphibian tetrapods of the paraphyletic group 'temnospondyli' (95 per cent of the trackways), as represented by the ichnogenus *Limnopus*. The ichnogenera *Dimetropus*, *Ichniotherium* and *Hyloidichnus* represent a smaller, relatively low diversity amniote assemblage (5 per cent), of inferred ophiacodontids, diadectomorphs and varanopsids, sphenacodontids or procolophonids respectively.

The later Moscovian Enville Member yielded a smaller assemblage, comprised of the ichnotaxa *Limnopus* (*Limnopus*) *vagus*, *Limnopus* (*Batrachichnus*) *salamandroides*, *Dimetropus leisnerianus*, and *Dromopus lacertoides*. Stem-lissamphibians remain the dominant biotaxa, although their representatives within the Enville Member are larger, perhaps reflecting the drier habitat. The typically semi-arid indicator ichnotaxon *Dromopus*, the postulated trackways of the Araeoscelididae, add further support to the hypothesis that changes in ichnotaxon diversity through the Salop Formation reflect a general drying trend from the lower Alveley to upper Enville Member, perhaps associated with climate change during the latest Carboniferous. Plant material and sedimentary structures also reflect the transition from humid, Late Carboniferous environments dominated by stem-lissamphibians and lycophytes, to Permian habitats comprising mainly amniotes, conifers, and marattialean tree-ferns within a semi-arid setting.

Ichnospecies concepts and numerical taxonomy

Ichnotaxa, as inorganic units, should be classified according to purely morphological, phenetic methods. Phylogenetic analysis of trackway data provides no insight into evolutionary relationships and produces paraphyletic groups with regard to trackmaker phylogeny. Consequently, phenetic analysis has been used to identify ichnotaxa within a hitherto partially described assemblage. The use of numerical methods increased the accuracy of ichnofaunal identification, with the intention of providing a stable ichnotaxonomy upon which further classifications, predictions and comparisons can be based. Using this method, the validity of previous vertebrate trackway designations is open to investigation under phenetic multivariate analysis with the use of the corresponding type specimens. In addition, undescribed trackways from other problematical ichno-assemblages can be more reliably classified by numerical comparison of their character morphology with that of type specimens associated with the ichnotaxa identified during *a priori* sorting. Phenetic analysis is a useful tool with which to rigorously test and refine ichnotaxonomic groupings, as exemplified by the numerical study of the Alveley ichno-assemblage. With the aid of such statistical, objective methods, the ichnotaxonomy of this assemblage has been stabilized, enabling an accurate estimation of ichnospecies diversity, under which, clear comparisons may be made with Early Permian ichnofaunas. Importantly, however, as with the use of all numerical methods in palaeontology, multivariate analysis must not be relied upon in isolation for vertebrate trackway identification and classification. Ichnotaxonomic schemes must always be founded upon detailed study of the original material with the *support* of statistical, numerical evidence.

Close examination of the results of multivariate cluster analyses shows that the difference between ichnospecies can often be based predominantly upon size, particularly within *Limnopus*. Whilst this is a useful character with which to describe morphological trends within the entire dataset, it is not suitable as an ichnotaxonomically diagnostic character. Ichnogenera, however, are more congruent with biotaxa. This agrees with similar statements made by workers on other trackway groups (e.g. Baird 1952; Weems 1990). Therefore, although the concept of trackway ichnospecies is essential for accurate specimen description, ichnogenera alone should be used for working comparisons with skeletal and other ichnological material.

The ichnofauna of the Late Carboniferous assemblage from Alveley, Shropshire, UK, is dominated by trackways of the ichnogenus *Limnopus* (95 per cent of the total ichnofauna), which is here redefined to incorporate two ichnosubgenera, *Limnopus* (*Limnopus*) and *Limnopus* (*Batrachichnus*). These ichnosubgenera are introduced here as a means of expressing the significant morphological similarity between *Limnopus* and *Batrachichnus*, whilst recognising that they are most likely of different trackmaker origin.

Trackways meet trackmakers: the correlation of ichnotaxa with biotaxa

The combination of trackway and body fossil data is best achieved when ichnological classifications are based upon the morphological features of trackways that relate directly to trackmaker anatomy and not to sedimentary or ethological influences. Trackways cannot be attributed to biotaxa with any degree of certainty without the use of synapomorphy-based, phylogenetic methods, in conjunction with phenetic and coincidence correlation techniques.

The identified groups of likely trackmaker candidates for common Late Palaeozoic ichnotaxa are predominantly familial, or of higher rank (such as in the case of the attribution of *Ichniotherium* to the class Diadectomorpha). In addition, only in a few cases can an ichnogenus be firmly assigned to any single monophyletic group, and generic assignations as specified by many authors are highly speculative. This highlights the fact that even under a purely morphological, numerical trackway classification, ichnotaxa do not mirror biotaxa, and an ichnological classification does not provide any insight into evolutionary relationships without combining the data with synapomorphy-based, phylogenetic analyses. Nevertheless, the method described is the optimal approach given the available data. Identification to family, or perhaps class level is possible, and this can still be useful in palaeoecological and biomechanical studies.

Taxon displacement and adaptive radiation in terrestrial tetrapod communities

The succession of stem-lissamphibians by amniotes as the dominant taxa of the Late Palaeozoic was considered using a synthesis of new and revised trackway data from Europe and North America, in conjunction with body fossil data. Trackway analyses demonstrate progressive clade displacement of Lissamphibia by Amniota, which is congruent with taxonomic richness curves newly compiled for the purposes of this study. Four models were therefore reviewed and tested to explain the observed pattern of Late Palaeozoic tetrapod faunal turnover: competitive taxon displacement; amniote expansion through 'key adaptations'; a change in stem-lissamphibian habitats; and Late Palaeozoic climate change. A new model for Late Palaeozoic faunal turnover was formulated, based upon trackway data and the new taxonomic richness curves. It was concluded that the intrinsic effects of competition and amniote expansion together acted with the extrinsic processes of extinction and climate change to produce the patterns of stem-lissamphibian and amniote diversity and abundance observed within successive trackway assemblages and in the body fossil record.

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APPENDIX 1

DATABASE OF TRACKWAY MEASUREMENTS USED FOR NUMERICAL TAXONOMY (ON CD)

This appendix is a database of measurements taken from specimens of the Alveley vertebrate ichno-assemblage, to be used for a numerical systematic analysis. Although many more characters and trackways were recorded, only those that were used in the multivariate cluster analysis outlined in Chapter 2 are included here.

APPENDIX 2

DEFINITION OF CONTINUOUS AND BINARY CHARACTERS USED IN TAXONOMIC ANALYSIS

= suspected extra-morphological features not used in multivariate cluster analysis

Continuous (quantitative) characters

1. MFL, PFL - Footlength (manus, pes). Length of foot from centre of base of heel to level of tip of longest digit. Measured along line of digit III.
2. MFW, PFW - Footwidth (manus, pes). Width of foot between tips of two outer digits.
3. MS, PS - Stride (manus, pes). Distance between tip of digit III of a footprint and tip of digit III of preceding, corresponding print of foot on the same side of the body. Represented in locomotion by 'a pendular movement of the leg, which is completed when the foot regains its starting position' (Leonardi 1987). The distance covered during this movement is the distance measured upon the resulting trackway. Hence, the value of stride is directly proportional to trackmaker velocity.
4. MP, PP - Pace (manus, pes). Distance between tip of digit III of a footprint and tip of digit III of corresponding print of foot on other side of body. In other words, the distance between impression of the right and left manus, or right and left pes.
5. M-PD - Manus–pes distance. Distance between tip of digit III of manus and tip of digit II of pes, within a single manus–pes set.
6. MTW, PTW - Trackwidth (manus, pes). Width of trackway measured between tip of digit III of a footprint and line joining tips of digit III of corresponding print of foot on other side of body.
7. Mα, Pα - Pace angulation (manus, pes). Angle between two consecutive measurements of pace. This value is directly proportional to trackmaker velocity. Observations on modern species have shown that pace angulation may vary according to age, sex, health (especially bone fractures) and gait. Therefore pace angulation is not reliable as a taxonomically diagnostic character. Note that manus pace angulation is greater than pes pace angulation if manus prints are closer to the trackway midline than the pes prints.
8. Mγ, Pγ - Print angulation (manus, pes). Angle nearest trackway midline, between line cutting trackway midline perpendicularly and meeting footprint at heel base, and line dissecting digit III, passing through tip of digit III and heel base. The precise value of print angulation may vary with the speed of the trackmaker. However, the general direction of print angulation (prints facing towards the trackway midline, away from the trackway midline, or parallel with the trackway midline) may still be used diagnostically.
9. M-PO - Manus–pes overlap. The overlap of the manus print by the succeeding pes print. Calculated using manus footlength – manus–pes distance. Negative number indicates no overlap, i.e. a positive distance between manus heel and pes digit III.

10. MθI, MθII, MθIII, PθI, PθII etc. - Digit divarification (manus, pes, digits I – IV / V). Angle between consecutive digits. Angle focus at base of digit I. Known to vary widely across groups (Peabody 1959) and therefore not suitable as a diagnostic character.
11. MDI, MDII, MDIII, PDI, PDII etc. - Digit length (manus, pes, digits I – IV / V). Length of digit from base at heel to tip, measured along centre of digit.
12. MHXI, MHXII, MHXIII, PHXI, PHXII, etc. - Digit hypex lengths (manus, pes, digits I – IV / V). Also known as the 'free length'. Length of digit from mid-point of the distance between two adjacent hypices to the digit tip.
13. # MBI, MBII, MBIII, PBI, PBII, etc. - Basal digit width (manus, pes, digits I – IV / V). Width of digit at line passing through two adjacent hypices, with the measured digit at the centre. Values are easily altered by extra-morphological features. This can be particularly misleading in smaller trackways, as any extra-morphological differences are more noticeable, occupying a larger proportion of the total value.
14. # MDTI, MDTII, MDTIII, PDTI, PDTII, etc. - Digit tip width (manus, pes, digits I – IV / V). Width of digit measured two millimeters from digit tip. As above, values are easily altered by extra morphological features, and this can be particularly misleading in smaller trackways.
15. MHL, PHL - Heel length (manus, pes). Length of heel from base to horizontal line passing through lowest observed bifurcation points between digits II and III, and digits III and IV (in five digit prints), or to lowest observed bifurcation between digits II and III in four digit prints. Used only for plantigrade prints.
16. MHW, PHW - Heel width (manus, pes). Width of heel at base, measured two millimetres from heel base if heel has a tapering or pointed morphology. Used only for plantigrade prints.
17. ST:FL - Stride: footlength ratio (manus, pes)

Qualitative (binary) characters

Note that absences (due to poor preservation or absent sections of trackway) are not marked with (0), but are instead not recorded. This is to prevent the clustering of characters recording a state of (1) together with absent characters.

1. NO - Digit number. Number of digits preserved and distinguishable: three (3); four (4); five (5).
2. # GRD - Footprint Grade. Reflects the extent to which the heel is used in locomotion, but may be affected by consistency of substrate and level of preservation of footprint. Tracks may be digitigrade (digit preserved only), semi-digitigrade (hypex length of digits and proximal part of heel preserved only) or plantigrade (entire foot preserved, including heel): digitigrade (1); semi-digitigrade (2); plantigrade (3).

3. # CRV - Digit curvature. Measured for each digit on a print. May be affected by consistency of substrate or speed of trackmaker. Known to vary widely across groups (Peabody 1959): curved towards trackway midline (1); straight (2); curved outwards from trackway midline (3).
4. # DTM - Digit tip morphology. Amphibians tend to have rounded digit tips whilst amniote trackways often show pointed digit tips. However, digit tip morphology is externally affected by substrate consistency, and the shape of the print may be altered as the foot is removed from the ground: rounded (1); pointed (2).
5. # DBM - Digit breadth morphology. Observed along digit length, from hypex to digit tip. Easily altered in appearance by extra-morphological features: tapering (1); uniform (2); widening (3).
6. # HM - Heel morphology. Shape of heel at base. May be affected by level of preservation of footprint, trackmaker speed and substrate consistency: rounded (1); tapering (2); square (3).
7. # SPM - Sole pad morphology. Amniote tracks often preserve sole pads, associated with protection of ossified carpals and tarsals; this feature is absent in amphibians. However, varying levels of preservation and substrate consistency may lead to the appearance of sole pads in amphibian tracks: absent (1); present (2).
8. # SM - Sole morphology. Refers to length of sole. Values may be affected by speed of trackmaker, substrate condition and method of preservation: short (1); elongate (2).
9. TAIL - Tail trace: absent (0); present (1).
10. TRK - Trackway pattern: regular (1); irregular (2).

APPENDIX 3

KEY TO SIGNS USED IN SYNONYMY LISTS

All synonymy lists are annotated following the recommendations of Matthews (1973), with minor amendments, as follows:

1881 Year in italics: this work has a mention of the species, but without description or illustration. It may be ignored by anyone who wishes to check merely the morphological information, rather than the total data arising out of the occurrence.

1881 Year in roman: the work contributes to our knowledge of the species. Illustrations: [kop. Anton 1856]: the illustration is not a new one, merely a repetition of one already produced by Anton in 1856. Someone who is familiar with the figure in the earlier work need not feel obliged to examine the repeat.

*1881 * in front of the year: with publication of this work the species can be regarded as valid under the terms of Article 11 of the ICZN.

.1881 . in front of the year: I accept responsibility for attaching this reference to the species under discussion.

?1881 ? in front of the year: the allocation of this reference must be subject to some doubt because of the way in which it was presented (e.g. if the species name concerned included at that time several forms now treated as separate species).

v1881 I have checked the deposited specimens that relate to the work cited, and on their evidence I have chosen the additional sign used. v*1881: I have seen the type of the species. v1881: because of the evidence of the deposited specimens we are able to take responsibility for this assignment.

p 1881 The specimens attributed to this reference apply only in part to the species under consideration (e.g. only three out of four figured specimens represent this species).

non 1881 Although a previous author has attributed figured specimens to the species under consideration, these specimens are here regarded to represent another species.

APPENDIX 4

TABLE OF TRACKMAKER FEATURES

(ON CD)

This appendix records features in Late Palaeozoic biotaxa that may potentially be recognised in their trackways. Taxa are organised according to the most recent, comprehensive phylogenies (Reisz 1986; Laurin 1993; Gaulthier 1994; Laurin and Reisz 1995; Lee 1995; Ruta *et al.* 2003). A list of references is given at the bottom of the page, together with stage name and geographical abbreviations. Digit length ratios serve merely to give an indication and are not considered to be highly precise.